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Early life and juvenile cephalopods around seamounts of the subtropical eastern North Atlantic: Illustrations and a key for their identification

by

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1. Abstract

Early life stages of cephalopod species were identified from zooplankton and nekton samples collected near seamounts of the subtropical eastern North Atlantic, especially at the Atlantis-Meteor Seamount Chain. Samples were taken during two recent German oceanographic expeditions into the region. In total, 1811 specimens, mainly posthatchlings and juveniles, were found, comprising 26 families and 49 species. A comprehensive species list is given as well as detailed illustrations of the major forms. A key was developed for an easy identification of the early life stages of oceanic cephalopods that dominated the cephalopod fauna from seamount regions of the subtropical eastern North Atlantic.

2. Introduction

Pelagic regions of the subtropical Atlantic Ocean are often regarded as „deserts", because they are characterised by low primary productivity and low standing stocks of zooplankton and nekton. However, there are various seamounts and islands in this region which may provide productive environments with appropriate conditions for all trophic levels of the marine food chain (Rogers 1994). As it has been shown for the Southwest Pacific, seamounts can harbour unique ecosystems that are inhabited by characteristic living communities and higher standing stocks of commercially exploitable pelagic and benthic fishes and invertebrates, which support traditional fishing grounds (Koslow 1997).

However, little is known about the distribution of cephalopods near seamounts, although these active pelagic predators are a major nektonic group occurring in all open oceans. They are essential elements of pelagic food chains (Piatkowski et al., 2001), their early life stages can occur in exceptionally high densities (Vecchione, 1999), and their distribution is often closely related to hydrographic conditions (Diekmann & Piatkowski, 2002). In the present study we examine a comprehensive collection of oceanic cephalopods sampled near various seamounts of the subtropical eastern Atlantic Ocean. They were caught with zooplankton nets and pelagic trawls during the Meteor-cruise M42/3 in September 1998, and the Heincke-cruise He135 in summer of 2000 (Fig. 1). The epi- and mesopelagic early life cephalopods of these expeditions are described in detail, the most abundant families and species are illustrated, and a key for their identification is given.

3. Materials and methods

Cephalopods were collected during two research cruises (Meteor 42/3, September 1998; and Heincke 135, August 2000) at four seamounts east of the Mid-Atlantic Ridge (Fig. 1). Sampling was conducted with zooplankton nets (BIOMOC (modified MOCNESS); 1m² opening; 335µm mesh size) and a pelagic youngfish trawl (YFT; 10x10m net opening; 11mm mesh size in the cod end) in different depths to a maximum depth of 950 m. All samples were initially preserved in 4% formalin, buffered with borax. 1811 cephalopods, essentially comprising early life stages, were sorted and identified to the lowest feasible taxonomic level. The cephalopod systematic followed the classification of Sweeney & Roper (2001) (see chapter 3, 4). Besides our own descriptions and illustrations, information and descriptions from Sweeney et al. (1992), Nesis (1987) and Roper et al. (1984) were considered for the identification key.

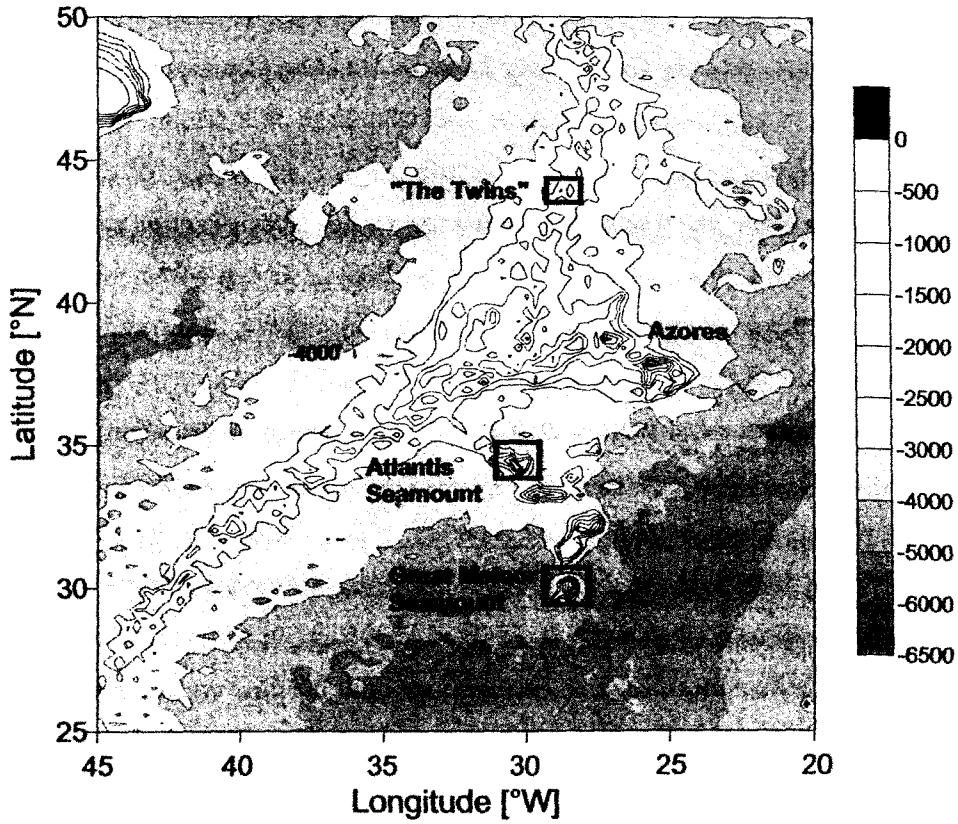
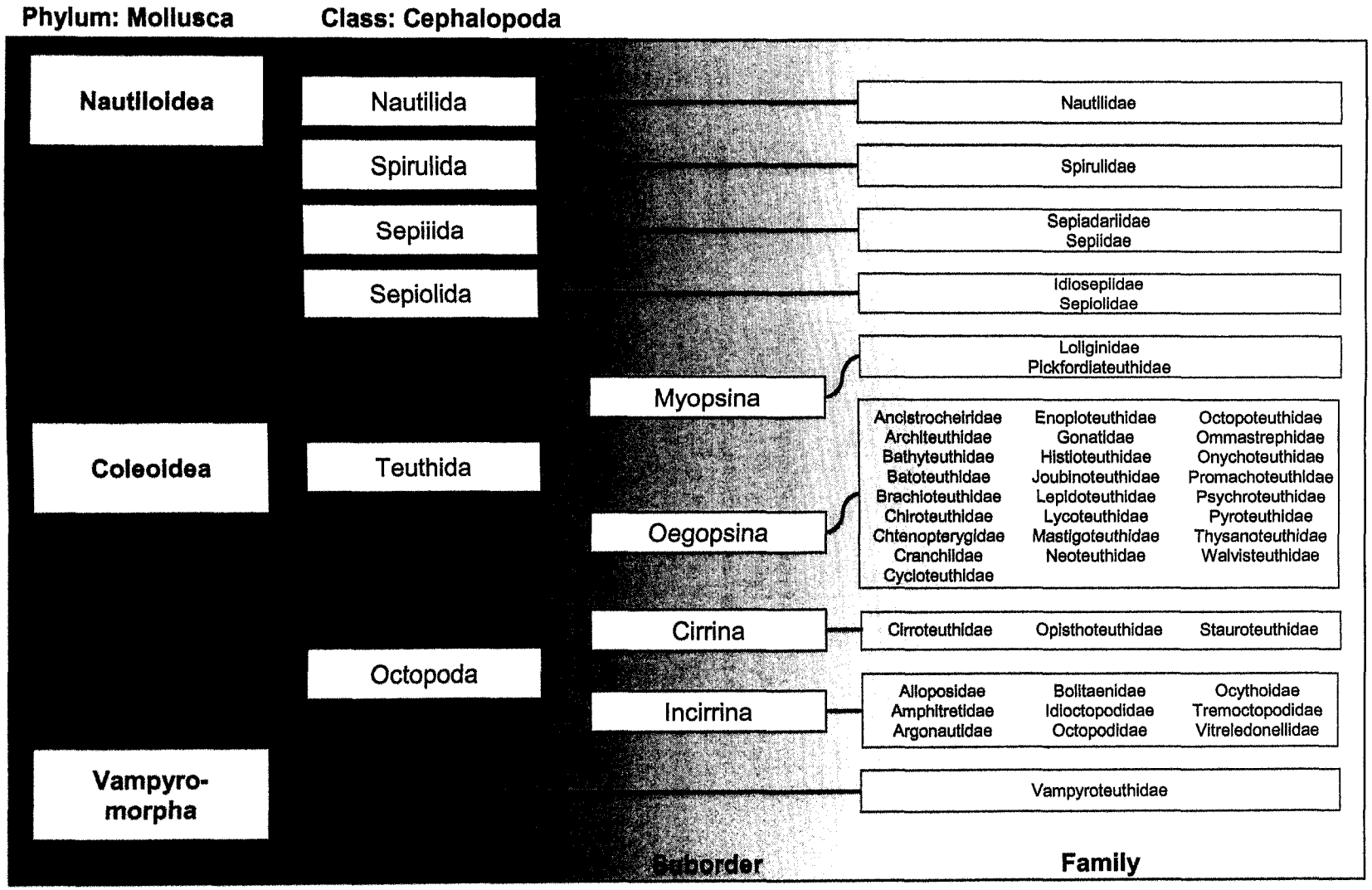


Fig. 1: Seamounts of the eastern subtropical North Atlantic investigated during two German research cruises (M42/3, HE135). Cephalopod early life stages and juveniles were sampled with zooplankton nets (Great Meteor Seamount only) and a pelagic youngfish trawl (all seamounts).



4. Classification of recent cephalopods (according to Sweeney & Roper (2001))

5. Checklist

Cephalopods around seamounts of the subtropical eastern North Atlantic:

Class Cephalopoda
Subclass Coleoidea
Order Spirulida
Family Spirulidae
Spirula spirula (Linnaeus, 1758)
Order Sepiolida
Family Sepiolidae
Subfamily Heteroteuthinae
Heteroteuthis dispar (Rüppel, 1844)
Order Teuthida
Suborder Oegopsina
Family Ancistrocheiridae
Ancistrocheirus lesueurii (Orbigny, 1842)
Family Bathyteuthidae
Bathyteuthis abyssicola (Hoyle, 1885)
Family Brachioteuthidae
Brachioteuthis riisei (Steenstrup, 1882)
Family Chiroteuthidae
Chiroteuthis sp. (Orbigny, 1841)
Grimalditeuthis bonplandi (Vérany, 1839)
Valbyteuthis sp. (Joubin, 1931)
[Synonymous to *Plancoteuthis* sp. (Pfeffer, 1912)]
Family Chtenopterygidae
Chtenopteryx sicula (Vérany, 1851)
Family Cranchiidae
Subfamily Cranchiinae
Cranchia scabra (Leach, 1817)
Liocranchia sp. (Pfeffer, 1884)
Leachia atlantica (Degner, 1925)
Subfamily Taoninae
Bathothauma lyromma (Chun, 1906)
Helicocranchia pfefferi (Massy, 1907)
Helicocranchia papillata (Voss, 1960)
Liguriella sp. (Issel, 1908)
Megalocranchia sp.(Pfeffer, 1884)
Taonius pavo (LeSueur, 1821)
Family Cycloteuthidae
Discoteuthis discus (Young & Roper, 1969)
Family Enoploteuthidae
Abralia veranyi (Rüppel, 1844)
Abraliopsis pfefferi (Joubin, 1896)
Enoploteuthis sp. (Orbigny, 1844)
Family Histioteuthidae
Histioteuthis arcturi (Robson, 1948)

Histioteuthis bonellii (Férussac, 1834)
Histioteuthis celetaria celetaria (Voss, 1960)
Histioteuthis meleagroteuthis (Chun, 1910)
Histioteuthis reversa (Verrill, 1880)
Family Lycoteuthidae
Subfamily Lampadioteuthinae
Lampadioteuthis megaleia (Berry, 1916)
Subfamily Lycoteuthinae
Selenoteuthis scintillans (Voss, 1959)
Family Mastigoteuthidae
Idioteuthis hjorti (Chun, 1913)
Mastigoteuthis atlantica (Joubin, 1933)
Family Octopoteuthidae
Taningia danae (Joubin, 1831)
Family Ommastrephidae
Subfamily Ommastrephinae
Ommastrephes bartramii (LeSueur, 1821)
Hyaloteuthis pelagica (Bosc, 1802)
Sthenoteuthis pteropus (Steenstrup, 1855)
Ornithoteuthis antillarum (Adam, 1957)
Family Onychoteuthidae
Onychoteuthis banksii (Leach, 1817)
Onykia carriboea (LeSueur, 1821)
Family Pyroteuthidae
Pterygioteuthis giardi giardi (Fischer, 1896)
Pyroteuthis margaritifera (Rüppel, 1844)
Family Thysanoteuthidae
Thysanoteuthis rhombus (Troschel, 1857)

Order Octopoda
Suborder Incirrina
Family Alloposidae
Alloposus mollis (Verril, 1880)
[Synonymous to *Haliphron atlanticus* (Steenstrup, 1861)]
Family Argonautidae
Argonauta argo (Linnaeus, 1758)
Family Bolitaenidae
Eledonella pygmaea (Verril, 1884)
Japetella diaphana (Hoyle, 1885)
Family Octopodidae
Subfamily Octopodinae
Octopus sp. (Cuvier, 1797)
Family *Ocythoidae*
Ocythoe tuberculata (Rafinesque, 1814)
Family Tremoctopodidae
Tremoctopus violaceus violaceus (Chiaje, 1830)
Family Vitrelledonellidae
Vitrelledonella richardi (Joubin, 1918)

Tab. 1: Early life stages of cephalopods collected with zooplankton nets (BIOMOC) and a pelagic youngfishtrawl (YFT) during the RV Meteor cruise 42/3 (September 1998) at Great Meteor Seamount (GMS) and during the RV Heincke cruise 135 (August 2000) at Atlantis Seamount, at "The Twins" and at a small seamount near the Azores. Numbers are absolute numbers, irrespective of effort and daytime. Numbers for higher taxa only include specimens that could not be further identified.

Order, Family	Species	GMS	GMS	Atlantis Seamount	"The Twins"	Azores
		N (Biomoc)	N (YFT)	N (YFT)	N (YFT)	N (YFT)
Order Spirulida						
Family Spirulidae	*Spirula spirula*		1			
Order Sepiolida						
Family Sepiolidae	*Heteroteuthis dispar*			6	12	3
Order Teuthida						
Sub-O. Oegopsina	Oegopsina indet.	183	6	5	2	
Family Ancistrocheiridae	*Ancistrocheirus lesueuri*	70				
Family Bathyteuthidae	*Bathyteuthis abyssicola*				1	
Family Brachioteuthidae	*Brachioteuthis* c.f. *riisei*	5	1		1	1
Family Chiroteuthidae	Chiroteuthidae indet.	2		1		
	Chiroteuthis sp.	11	1			
	Valbyteuthis sp.	8				
Family Chtenopterygidae	*Chtenopteryx sicula*	52	20	8	1	
Family Cranchiidae	Cranchiidae indet.	10				
Subfamily Cranchiinae	Cranchiinae indet.	8				
	Cranchia scabra	4	2		1	
	Leachia atlantica	1				
	Liocranchia sp.	2			1	
Subfamily Taoninae	Taoninae indet.	5				
	Bathotheuma lyromma	3		5	2	3
	Helicocranchia pfefferi	4	4	2	3	
	Helicocranchia papillata	21	2			
	Helicocranchia sp.	3	2			
	Liguriella sp.	3				
	Megalocranchia sp.			1	6	
	Taonius pavo			5	10	2
Family Cycloteuthidae	*Discoteuthis discus*	3		1	1	1
Family Enoploteuthidae	Enoploteuthidae indet.	136			1	
	Abralia c.f. *veranyi*	1	3			
	Abraliopsis pfefferi	86	106	9	39	
	Enoploteuthis sp.	7	6		1	
Family Grimalditeuthidae	*Grimalditeuthis* c.f. *bonplandi*		1			
Family Histioteuthidae	*Histioteuthis* sp.	1	1	4	1	
	Histioteuthis arcturi				6	
	Histioteuthis bonelli			4		
	Histioteuthis celetaria celetaria	1		4	1	
	Histioteuthis meleagroteuthis			2	3	
	Histioteuthis reversa			10		
Family Lycoteuthidae	Lycoteuthidae indet.	8				
Subfamily Lampadioteuthinae	*Lampadioteuthis megalops*		1	2	1	
Subfamily Lycoteuthinae	*Selenoteuthis scintillans*	54	20			
Family Mastigoteuthidae	*Idioteuthis* c.f. *hjorti*			3		
	Mastigoteuthis c.f. *atlantica*	3		1	3	1
Family Octopoteuthidae	*Taningia danae*				1	
Family Ommastrephidae	Ommastrephidae indet.	7	3	2	2	2
Subfamily Ommastrephinae	*Hyaloteuthis pelagica*	8	2			
	Ommastrephes bartramii	38	18	4	4	
	Ornithoteuthis antillarum	3				
	Sthenoteuthis c.f. *pteropus*	6				
Family Onychoteuthidae	Onychoteuthidae indet.	6				
	Onychoteuthis banksii	194	52	27	16	3
	Onykia carribaea	14				
Family Pyroteuthidae	Pyroteuthidae indet.	28	2			
	Pterygioteuthis giardi giardi	2	12	20	9	
	Pyroteuthis margaritifera	77	16	42	13	1
Family Thysanoteuthidae	*Thysanoteuthis rhombus*	8				
Order Octopoda	Octopoda indet.	1				
Sub-O. Incirrina						
Family Alloposidae	*Alloposus mollis*			1	1	
Family Argonautidae	*Argonauta argo*	21		1		1
Family Bolitaenidae	*Eledonella pygmaea*	43	5		2	
	Japetella diaphana				1	
Family Octopodidae	Octopus sp.	27				
Family Ocythoidae	*Ocythoe tuberculata*			3		
Family Tremoctopodidae	*Tremoctopus violaceus violaceus*	2	1			
Family Vitreledonellidae	*Vitreledonella richardi*		2	1	1	
Sum		1180	292	174	147	18

6. Identification key of early life stages of oceanic cephalopods in the eastern subtropical North Atlantic (identification to family level)

1. • mantle without fins; arm crown without tentacles ⇒ **Order Octopoda** ⇒ **21.**
   • mantle with fins or fin rudiments; one pair of tentacles or a trunk-like structure (proboscis) exists ⇒ **2.**

2. • mantle with lateral fins ⇒ **3.**
   • mantle with subterminal or terminal fins, sometimes dorsally attached ⇒ **Order Teuthida** ⇒ **4.**

3. • coiled chambered shell in posterior mantle; fins or fin rudiments tiny and widely separated; huge buccal mass; well developed beak ⇒ **Spirulidae**
   • no coiled chambered shell; each fin at least as wide as long; buccal mass inconspicious ⇒ **Sepiolidae**

Order Teuthida

4. • eye covered by a transparent membrane (cornea) ⇒ Sub.-O. Myopsina (no species of this suborder found around the seamounts)
   • eye without cornea, thus, in contact with seawater ⇒ Sub.-O.Oegopsina ⇒ **5.**

5. • tentacles fused into trunk like structure (proboscis) ⇒ **Ommastrephidae**
   • pair of tentacles; no proboscis ⇒ **6.**

6. • head with long neck ⇒ **7.**
   • head without long neck ⇒ **8.**

7. • neck with dorsal hump; arm crown not stalked ⇒ **Brachioteuthidae**
   • neck multiple chambered and without dorsal hump; long tail with secondary fin (often missing); arm crown stalked ⇒ **Chiroteuthidae**

8. • body elongated with long pointed tail; tentacles greatly enlarged/ streched; funnel locking-cartilage oval with small projection (tragus) ⇒ **Mastigoteuthidae**
   • other features than above; if body elongated and/ or tentacles enlarged the funnel locking-cartilage is permanently fused with the mantle ⇒ **9.**

9. • funnel locking cartilage and mantle permanently fused ⇒ **10.**
   • funnel locking cartilage and mantle not fused; mantle always free in nuchal region ⇒ **11.**

10. • mantle free in nuchal region ⇒ **Grimalditeuthidae**
    • mantle fused in nuchal region ⇒ **Cranchiidae**

11.• transverse T-shape funnel locking-cartilage; mantle densely covered with small chromatophores, even visible in preserved specimens ⇒ **Thysanoteuthidae**
• funnel locking-cartilage of other shape (straight, round or subtriangular) ⇒ **12.**

12.• fins with muscular ribs; tentacular club in small larvae spatulate, nearly round and out-turned; funnel locking-cartilage straight ⇒ **Chtenopterygidae**
• fins without ribs ⇒ **13.**

13.• mantle sharply pointed posteriorly; funnel locking-cartilage straight; head often withdrawn into mantle up to eye lenses; in young stages arm pair IV rudimentary ⇒ **Onychoteuthidae**
• features other than above ⇒ **14.**

14.• no photophores on the skin (external) nor on intestine ⇒ **15.**
• photophores on mantle, arms, head and/ or eyes and intestine ⇒ **16.**

15.• fins nearly oval in outline, grow up to 100% ML (*Discoteuthis*); fin musculature separated in the midline by the gladius; funnel locking-cartilage subtriangular; 4 rows and more than 15 suckers on club ⇒ **Cycloteuthidae**
• fins very broad in specimens >3mm ML; fin musculature not separated by gladius; funnel locking-cartilage straight; tentacles present only in early juveniles (<12 suckers on club), generally lost in later stages ⇒ **Octopoteuthidae**

16.• ventral side of mantle, head and arms covered with usually big photophores (late paralarval stages), which are directed anteriorly; left eye is considerably larger than the right one; integumental light organs around margin of eye lid ⇒ **Histioteuthidae**
• other structure and pattern of photophores; eyes of equal size ⇒ **17.**

17.• light organs at base of arms; entire animal of dark reddish-brown colour ⇒ **Bathyteuthidae**
• no light organs at base of arms but on mantle, arms and/ or eyes and intestine ⇒ "Enoploteuthid" group of families and Lycoteuthidae ⇒ **18.**

18.• no light organs on eyes ⇒ **Ancistrocheiridae**
• light organs on eyes, well defined even in youngest stages ⇒ **19.**

19.• no light organs on viscera ⇒ **Enoploteuthidae**
• light organs present on viscera but absent from surface of mantle, funnel, head and arms (not considering tentacles) ⇒ **20.**

20.• ventral surface of eyes with 3 to 5 light organs; central one develops first, is always enlarged and of different colour and surface texture ⇒ **Lycoteuthidae**
• ventral surface of eye with unequal sized light organs (12-15 light organs in older stages); young with very small tentacular clubs, that generally curl dorsally at the tip and are covered with small suckers ⇒ **Pyroteuthidae**

Order Octopoda

21.• mantle gelatinous; web between all arms ⇒ **22.**
• mantle muscular ⇒ **24.**

22.• eyes large and hemispherical; mantle to arm ratio 1:1; suckers uniserial within the deep web and biserial beyond ⇒ **Alloposidae**
• eyes smaller and of different shape than above; suckers on arms uniserial ⇒ **23.**

23.• eyes elliptical; web not very deep in youngest stages; mantle to arm ratio approximately 3:1; ovoid digestive gland; gelatinous mantle often appears "hairy" ⇒ **Bolitaenidae**
• eyes rectangular; mantle to arm ratio approximately 2:1; digestive gland very long and slender, pointed at the posterior end ⇒ **Vitreledonellidae**

24.• arms of equal length or only slightly enlarged ⇒ **25.**
• arm pairs I, or I and IV greatly enlarged ⇒ **26.**

25.• specialised funnel locking cartilage present (groove with a small knob below), conspicuous even in hatchlings; in young females arm pair I slightly enlarged; dwarfed males with hectocotylus enveloped in a small sac ⇒ **Argonautidae**
• no specialised funnel locking cartilage (roughly a small "bump"), mantle locking apparatus absent; arms not modified in young males; arms equal in length and generally short and compact ⇒ **Octopodidae**

26.• arm pairs I and IV greatly enlarged, in youngest stages not enclosed in brachial membrane; funnel elongated ⇒ **Ocythoidae**
• arm pair I greatly enlarged and robust, arm pair III reduced; in hatchlings head and arms enveloped by brachial membrane ⇒ **Tremoctopodidae**

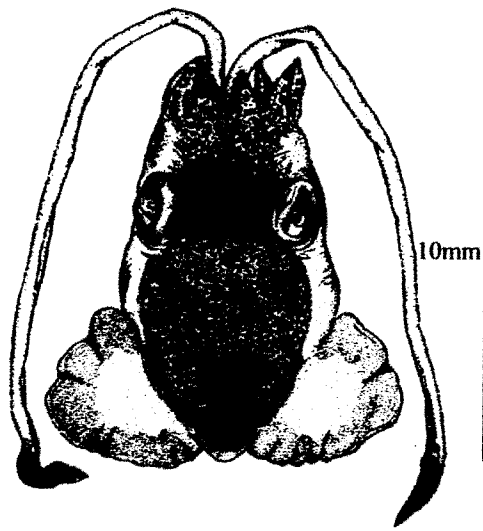
7. Description and illustration of major species

Order Spirulida
Family Spirulidae

Only one species, *Spirula spirula*, is recognised within this family. This cephalopod is small (up to 4.5cm ML) and distributed worldwide in tropical and subtropical waters. There are indications that *S. spirula* is associated with continental slopes and oceanic islands. The species is characterised by an internal shell, that is calcareous, coiled and chambered. The shell lies within the posterior half of the mantle and is already visible at 1.5mm ML (no metamorphosis during development). Fins are round and small. The arms are short and connected by a deep web. In hatchlings the head may be retracted entirely into the mantle. During further development the huge buccal mass becomes visible and fins are only recognisable as small rudiments.

Order Sepiolida
Family Sepiolidae

The family is characterised by a short, broad mantle with large, round fins. The funnel locking-cartilage is simple and straight. The shell is reduced to a chitinous gladius or completely absent. Adults are relatively small in body size. Only one species (*Heteroteuthis dispar*) was identified at the seamounts of the subtropical eastern North Atlantic.



H. dispar (Subfamily Heteroteuthinae, Fig. 2) is characterised by a deep web, joining the first three pairs of arms. The ventral arms are not connected. Fins are large and extend to the posterior end of the mantle. The dorsal edge of the mantle is free (not fused like in some related species). The light organ inside the mantle cavity (partly covered by the funnel) is rounded. The maximum mantle length of *H. dispar* is around 2.5cm (Bello, 1995).

Fig. 2: ***Heteroteuthis dispar***. Dorsal view of juvenile (ML=11mm)

Order Teuthida, Suborder Oegopsina

Enoploteuthid group of families:

The Enoploteuthidae, Ancistrocheiridae and Pyroteuthidae have traditionally been classified as subfamilies within the family Enoploteuthidae (Pfeffer, 1912). According to Clarke (1988) and Young & Harman (1998) they are now treated as separate families and are currently comprised to the enoploteuthid group of families. Because of some similarities in the identification characteristics the Lycoteuthidae are discussed together with the enoploteuthid group:

The representatives of all four families are small to medium sized squids. They are widely abundant but of minor importance to fisheries. Common to all is their mesopelagic lifestyle and the extended diurnal vertical migrations performed by the adults. In older stages hooks can be found on arms (two rows) and tentacular clubs (one or two rows; apart from the genus *Pterygioteuthis*).

Families of the group are characterised by highly complex photophores and can be distinguished by their arrangement and numbers on various body parts (Tab. 2).

Tab. 2: Key to families of the enoploteuthid group and the Lycoteuthidae based on photophore patterns

Photophores	Enoploteuthidae	Ancistrocheiridae	Pyroteuthidae	Lycoteuthidae
Mantle, head, arms	+ (in rows)	+	–	(arms & tentacles partly with integumentary ph.)
Tentacles	–	+	+ (embedded in stalk)	
Eyes	+	–	+	+
Viscera	–	–	+	+

Family Enoploteuthidae:

The Enoploteuthidae are among the most abundant small squids of the open ocean. Three of the four genera (*Enoploteuthis, Abralia, Abraliopsis*) are distributed in the Atlantic Ocean and are especially numerous in the subtropical region (Nesis, 1987). Several small photophores on the ventral side of the mantle and head are mostly arranged in rows. Young stages are difficult

to separate, because the characteristic photophore patterns do not develop before 4-5mm mantle length.

Table 3 comprises characteristics to distinguish between the two genera *Abralia* and *Abraliopsis*.

Tab. 3: Key to the early life stages of the genera *Abraliopsis* and *Abralia* (partly following Young et al., 1992)

	Abraliopsis sp.	*Abralia* sp.
Arms, tentacles	Extremely long, sometimes as long as or longer than mantle length	Very long, never longer as mantle length
Arm formula	III > II > I > Iç (3mm ML) Iç > III > II > I (juveniles)	II > I > III > Iç
Iç arm pair	3 terminal light organs (~black), first visible as swelling	No light organs on armtips
Photophores on eyes	5 photophores; 1>5>3 develop first; anlagen 2 and 4 visible juveniles: photophores of similar structure. Size: 1 = 5 > 2 = 3 = 4	5 photophores; 1>5>3 develop first; no anlagen visible juveniles: posterior photophore different from others

***Abralia* cf. *veranyi*:**

Abralia veranyi is distributed in the tropical and subtropical eastern and western North Atlantic Ocean and the Mediterranean Sea. It is associated with the continental shelf and does not occur in the open ocean. Nevertheless a few specimens were recognised around seamounts of the Atlantis-Meteor Chain. In addition to the features listed in Table 3 late juveniles and adults of the genus *Abralia* are characterised by one series of hooks and two series of suckers on the manus of the club.

Abraliopsis pfefferi (Fig. 3)*:*

The distribution of *Abraliopsis pfefferi* is limited to the tropical and subtropical Atlantic Ocean as also to the adjacent seas of the Gulf of Mexico and the Mediterranean (Nesis, 1987). Along the seamounts of the Mid-Atlantic Ridge the genus *Abraliopsis* was the most abundant enoploteuthid squid and dominated, aside from *Onychoteuthis banksii*, the cephalopod fauna.

The genus *Abraliopsis* is the easiest enoploteuthid to identify. It is characterised by three conspicuous dark photophores (green in living specimens) on the tip of the 4th armpair. Arms and tentacles are extremely long and mostly exceed mantle length. In juveniles and adults five round photophores of similar structure develop on the ventral side of each eye. They form a

typical row with the posterior and anterior photophore enlarged. The manus of the club is armed with two series of hooks.

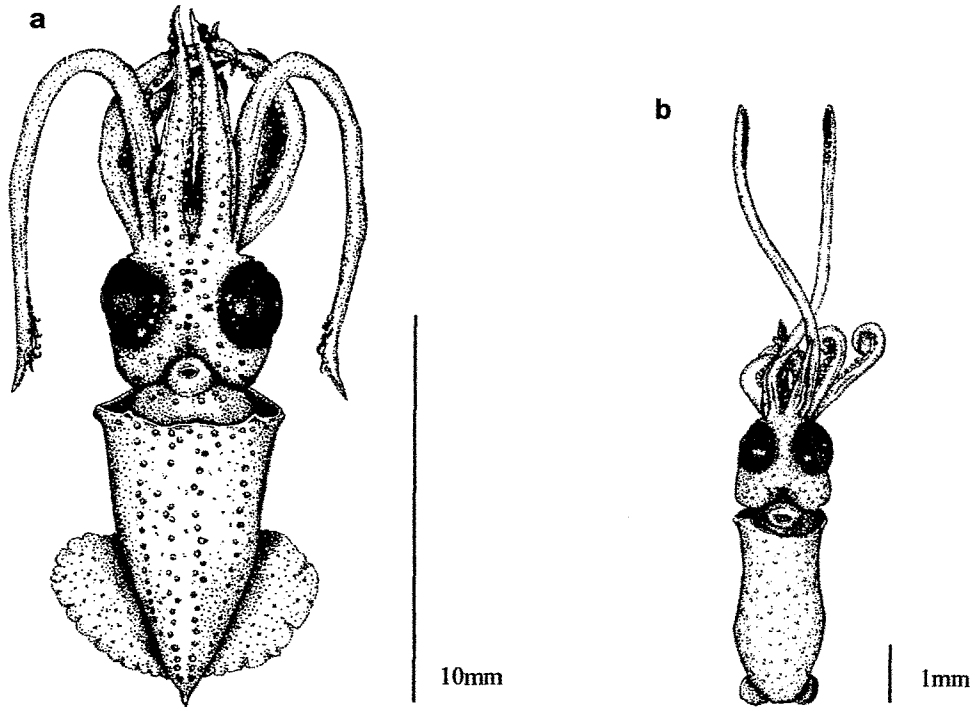


Fig. 3: ***Abraliopsis pfefferi***
Ventral view of (a) late juvenile (ML=8.5mm) and (b) early juvenile (ML=3.6mm)

***Enoploteuthis* sp.** (Fig. 4):

Similar to the other two enoploteuthid species *Enoploteuthis* or the species *E. leptura leptura*, respectively, is distributed in the tropical Atlantic Ocean, from Bermuda to Madeira and Brazil to southwestern Africa (Nesis, 1987). Adults display a similar photophore pattern on the eyes as *Abraliopsis*, with the posterior and anterior one enlarged and the remaining three photophores small. In Hawaiian species of this genera the development of the ocular photophores begins with the two enlarged photophores. Apart from the other genera, *Enoploteuthis* is characterised by a tail-like projection beyond the posterior end of the fins. It can be detected at a mantle length of 10-15mm (Young et al., 1992). The manus of the tentacular club is armed with two series of hooks.

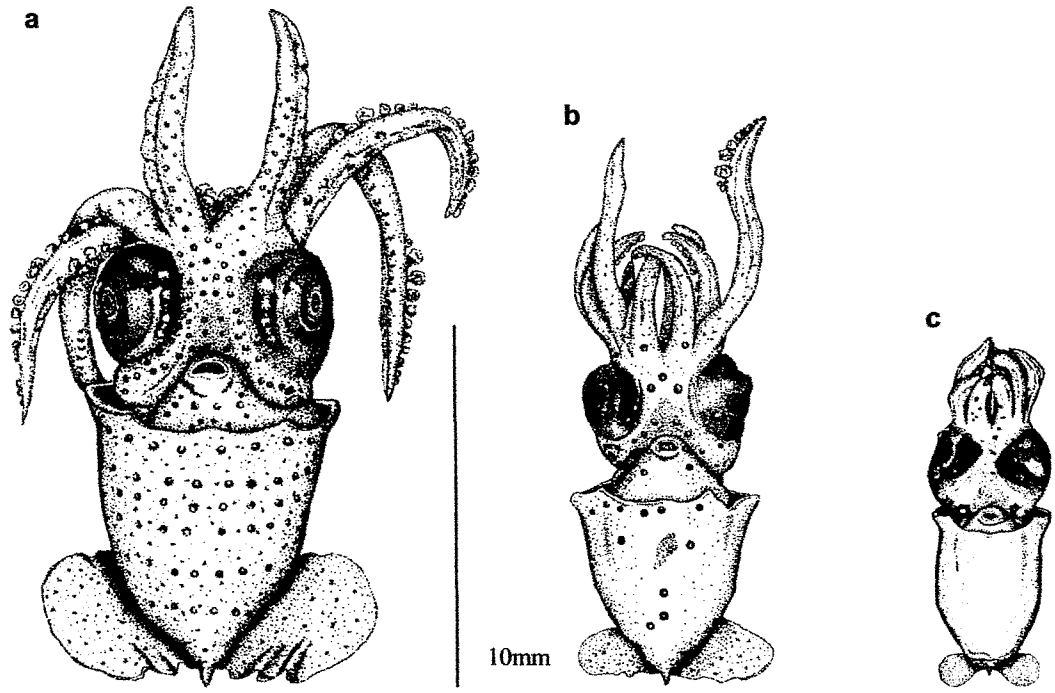


Fig. 4: ***Enoploteuthis* sp.**
Ventral view of (a) late juvenile (ML=9.2mm), and early juveniles (b) ML=5.5mm), (c) ML=4.3mm

Family Ancistrocheiridae:

Only one species, *Ancistrocheirus lesueurii*, is currently recognised in this family. It is circumglobally distributed but mainly restricted to tropical and subtropical waters. Differences in the morphology of early life stages from various oceans suggest, that more than one species exist (Young et al., 1992).

A. lesueurii can be easily distinguished from all other forms of the enoploteuthid group. Eyes are small, separated from the arm bases and are widely divergent. The head tissue is gelatinous. Tentacles are covered with photophores (not in youngest stages) and the tentacular club bears a few but very large suckers (Fig. 5).

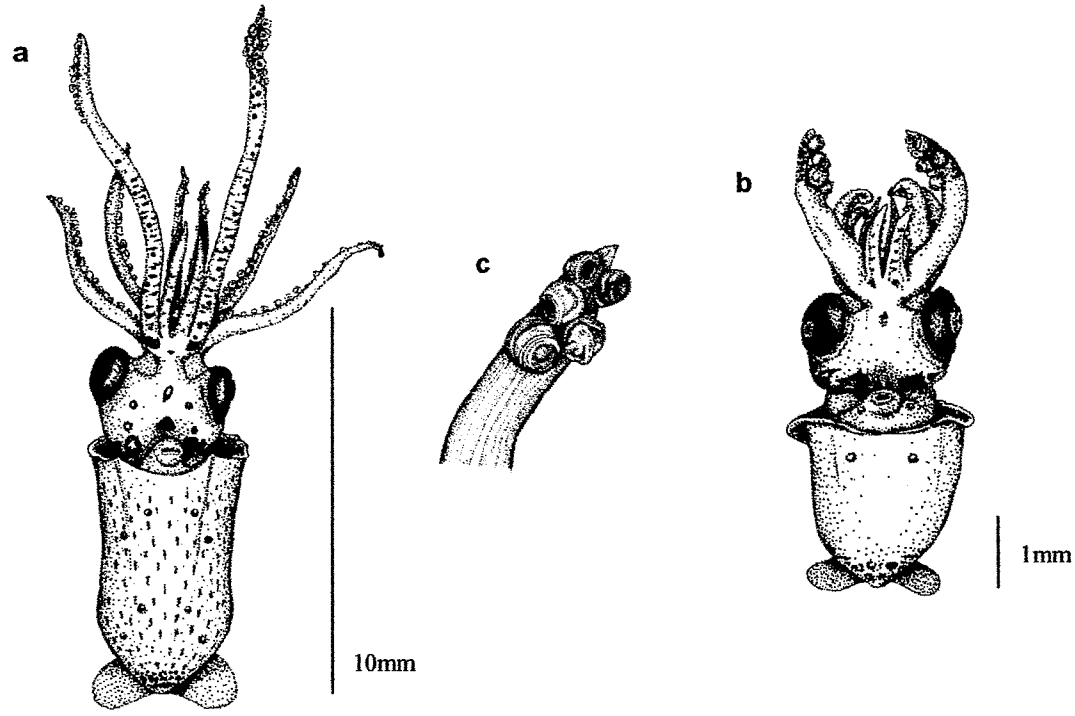


Fig. 5: ***Ancistrocheirus lesueurii***
Ventral view of (a) juvenile (ML=6.9mm), (b) early juvenile (ML=2.8mm) and (c) tentacular club of juvenile (ML=1.9mm)

Family Pyroteuthidae:

Two genera (*Pyroteuthis, Pterygioteuthis*) are comprised in this family. Pyroteuthids are cosmopolitan mesopelagic species and are mainly found in tropical to subtropical waters. Their paralarvae are among the most abundant cephalopods in the plankton.

In addition to the photophore patterns, described in Table 4, young specimens of this family are characterised by very small tentacular clubs that generally curl at the tip and are covered with very small suckers. The tentacular stalk usually has a ventrally directed bend. In specimens larger than approximately 5mm ML the posterior end of the mantle is sharply pointed, the terminal conus of the gladius becomes visible (equivalent to the adults) and the fins show their typical appearance (rounded with two free lobes).

The two genera can be distinguished following Table 4.

Tab. 4: Key to the genera *Pyroteuthis* and *Pterygioteuthis*

	Pyroteuthis	*Pterygioteuthis*
Gill photophores (<4-5mm ML)	absent	Present (at 1.5mm ML)
Gill photophores (>5mm ML)	Smaller than anal photophores	As large or larger than anal photophores
tentacle (freshly caught specimens)	Pink patch at the base of each tentacle and at the carpus	No pink patches

Early life stages of these genera can be hardly identified to species. Nevertheless, additional catches of larger Pyroteuthidae at the same locations allowed to identify the species *Pyroteuthis margaritifera* and *Pterygioteuthis giardi giardi* (Fig. 6) in the plankton catches of the subtropical eastern North Atlantic.

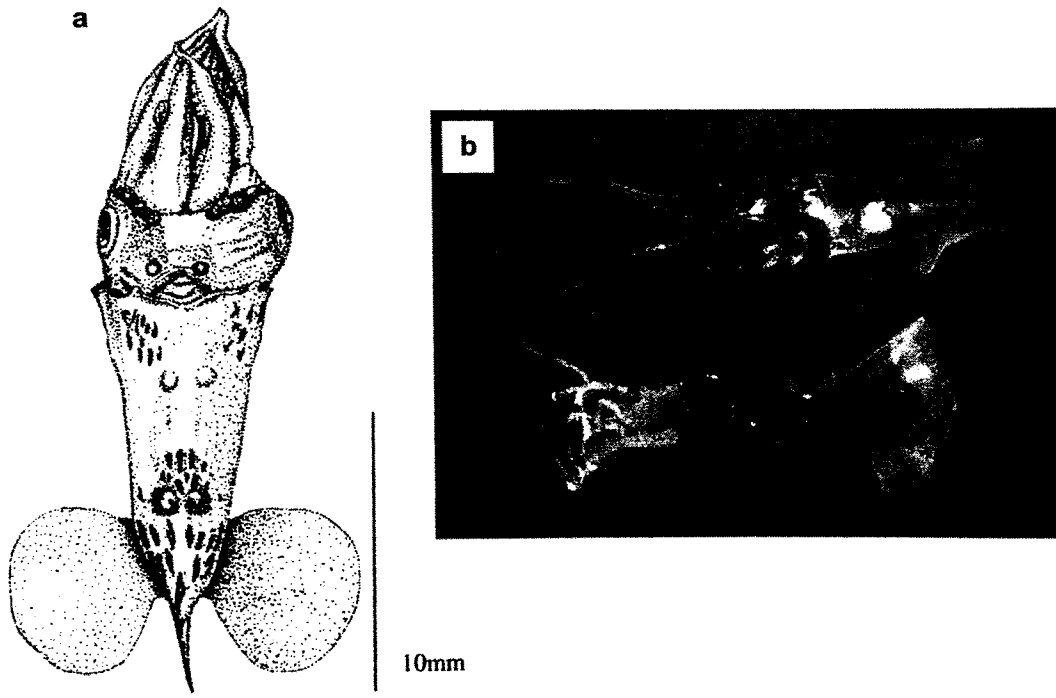


Fig. 6: **Pyroteuthidae**
(a) ***Pterygioteuthis giardi giardi***; ventral view of adult (ML=14mm); (b) ventral view of adult ***Pterygioteuthis giardi giardi*** (top) and ***Pyroteuthis margaritifera*** (bottom)

Family Lycoteuthidae

Young Lycoteuthidae are relatively easy to separate from the enoploteuthid group by the early development of one large and exceptionally coloured photophore on the centre of each eyeball (apart from *Lampadioteuthis megalaia*). Two species of two subfamilies occurred in the eastern subtropical North Atlantic Ocean. They are identifiable by the arrangement and the colour of the photophores around their eyes:

- Subfamily Lampadioteuthinae: This monotypic subfamily (*Lampadioteuthis megaleia*) is currently known from the subtropical waters of the western South Pacific and the North Atlantic. *L. megaleia* is characterised by four photophores on the eyeball: Three are in a line, the fourth is positioned posterior to the other photophores and next to the eye lens.
- Subfamily Lycoteuthinae: Only one species was recognised in the subtropical East Atlantic. *Selenoteuthis scintillans* (Fig. 7) is characterised by the early development of three photophores on the ventral periphery of each eye. The central photophore is markedly larger than the others and of a different structure and colour (even recognisable after preservation). On the posterior end of the mantle one large globular photophore is visible, that darkens in later developmental stages.

S. scintillans is a small-bodied squid (up to 4.5cm ML in adults), which is widely distributed in the tropical and subtropical Atlantic, with lower abundances in the eastern part.

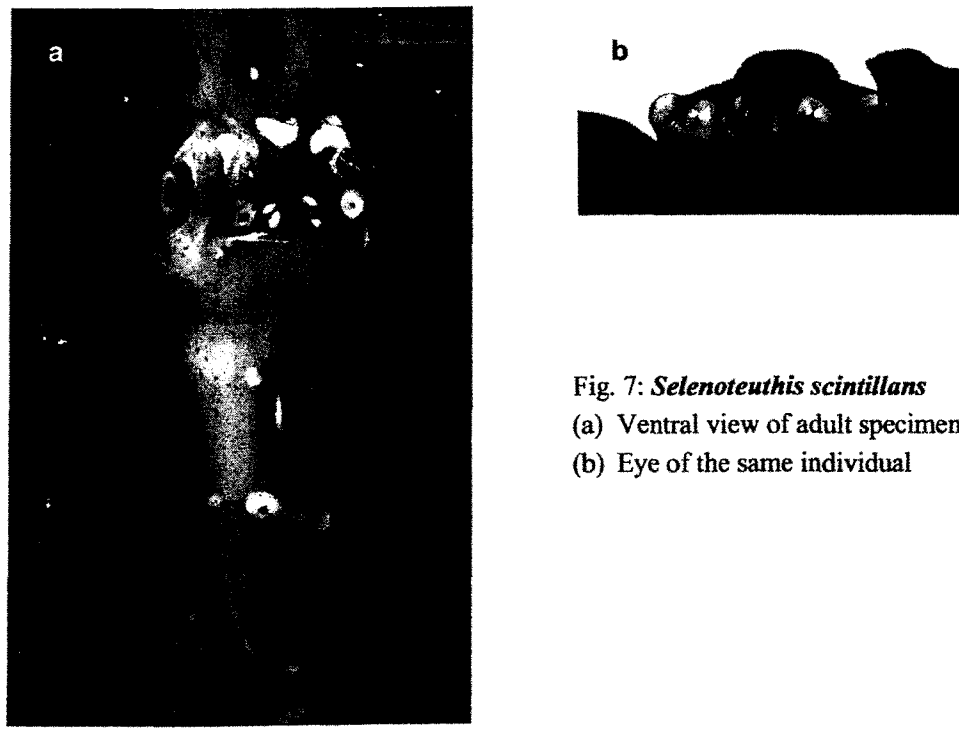


Fig. 7: ***Selenoteuthis scintillans***
(a) Ventral view of adult specimen (ML~30mm),
(b) Eye of the same individual

Family Histioteuthidae

Histioteuthidae are medium to large-bodied squids, that occur worldwide apart from the Arctic and Antarctic. They are meso- to bathypelagic and some species apparently show association with continental slopes, islands, and seamounts. The family is currently under revision (N. Voss, pers. comm.). 13 species in a single genus are recognised so far. Early life stages are problematic to distinguish on the species level. Generally juveniles may be identifiable at 10mm ML or above. The advanced literature should be consulted for detailed species characteristics (e.g. Voss, 1969; Voss et al., 1998). Nevertheless, the family can be easily separated from other oegopsid families at nearly all developmental stages.

Typical family characteristics are (see also Fig. 8):
Conical and short mantle; mantle tissue usually thick and firm; skin colour of juvenile to adult specimens brownish red; head large; in older specimens eyes large and asymmetrically developed with the left eye larger than the right one; numerous compound photophores, anteriorly directed, on mantle (often in diagonal rows), head and arms.

Fig. 8: ***Histioteuthis celetaria celetaria***
Ventral view of juvenile specimen
(ML=7.1mm)

Family Ommastrephidae

The Ommastrephidae or "Flying squids" are an oceanic and neritic family representing powerful swimmers. Six of the ten genera currently support a fishery and the family is supposed to be the most important commercial oceanic cephalopod group. The fertilised eggs are released and encapsulated in large gelatinous egg masses, which are probably pelagic. The hatchling is characterised by a distinctive paralarval form, the "rhynchoteuthion". In this developmental stage the tentacles are fused into a trunk-like structure, the proboscis. As the squid grows, the proboscis begins to divide with a splitting groove forming at its base. The separation into the two tentacles is completed at a mantle length of 6-10mm, depending on species (Tab. 5).

Four genera/ species of this family occur in the oceanic regions of the subtropical North Atlantic and around the investigated seamounts. The most common species in the samples was *Ommastrephes bartramii* (Fig. 10). *Hyaloteuthis pelagica* (Fig. 9), *Sthenoteuthis* c.f. *pteropus* and *Ornithoteuthis antillarum* were only found sporadically.

Identification to species level is still tentative. Table 5 is a first approach to distinguish between the four paralarval forms.

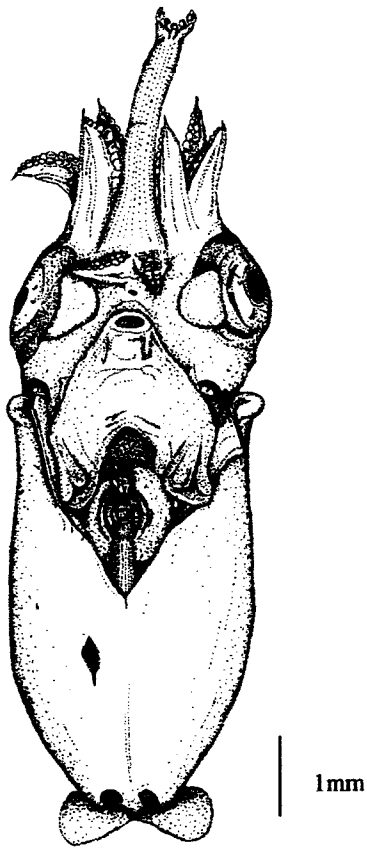


Fig. 9: ***Hyaloteuthis pelagica***
Ventral view of rhynchoteuthion paralarva (ML=4.3mm);
parts of mantle removed, to show the single round photophore centrally located on intestine

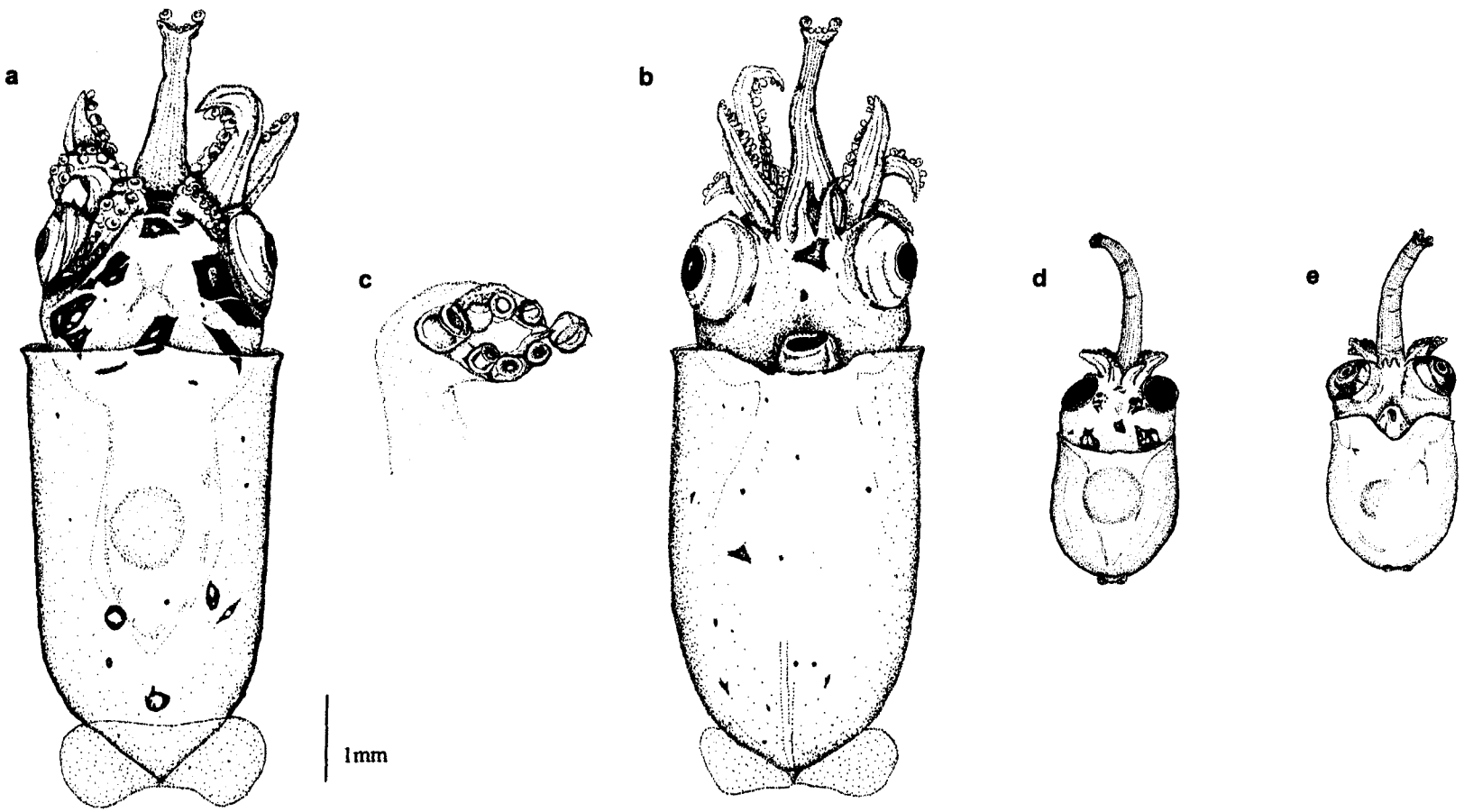


Fig. 10: ***Ommastrephes bartramii***
Dorsal (a) and ventral (b) view of rhychoteuthion paralava (ML=5.2mm), (c) end of proboscis of the same specimen; dorsal (d) and ventral (e) view of hatchling (ML=1.4mm)

Tab. 5: Summary of characters of early young stages of ommastrephids. Data are based upon own measurements and workshop studies as described in Wormuth et al. (1992).

	Ommastrephes bartramii	*Hyaloteuthis pelagica*	*Ornitoteuthis antillarum*	*Sthenoteuthis pteropus*
lateral suckers	enlarged approx. 200%	enlarged to >= 150%	enlarged up to 150%	slightly enlarged, sometimes invisible
Proboscis length *	approx. 100% ML	up to 80%	approx. 50%	up to 80 - 90%
Photophores on eyes	photogenic tissue	large, round photophore	round photogenic tissue	large round photophore
Photophores on intestine	absent	one large round photophore (ML >=1.5mm)	two photophores, posterior one larger than anterior (difficult to observe)	two photophores of similar size, development probably later than 3,0mm ML (difficult to observe)

* before beginning of the proboscis division

Family Onychoteuthidae

Two species, *Onychoteuthis banksii* and *Onykia carriboea*, occur in the eastern subtropical North Atlantic. Both are distributed worldwide.

Onykia carriboea (Fig. 11) is a small, broad-bodied squid, frequently found in surface collections from warm-water masses. The mantle is almost bullet-shaped and not as sharply pointed as in *Onychoteuthis* (see below). Photophores are absent. Mantle, head, tentacles, arms and funnel of paralarvae are densely covered with chromatophores (>3mm ML). Most striking are the characteristic dark chromatophores on the dorsal midline of the mantle, which increase in size from anterior to posterior and can be easily recognised also in preserved specimens. All cephalopods identified as *O. carriboea* so far have been immature. This suggests that the species may only represent an immature growth stage of another onychoteuthid species (Tsuchiya & Okutani, 1991; Kubodera et al., 1998).

Onychoteuthis banksii (Fig. 12) is probably a complex of several species (Young, 1972; Young & Harman, 1987). Specimens are muscular, fins are rhomboidal and the tail is pointed. Tentacular clubs of juveniles and adults bear 19 to 23 claw-like hooks in two rows. *Onychoteuthis* is considered to be a fast-growing squid. The paralarvae can be easily identified by their muscular body and their visible, sharply pointed gladius. One patch of photogenic tissue, a developing photophore, can be sometimes recognised on the ventral side of the eyes. In very young specimens hooks cannot be seen or are just partly developed. Two large round, bulbous light organs along the ventral midline on intestinal tract will develop in grown up specimens.

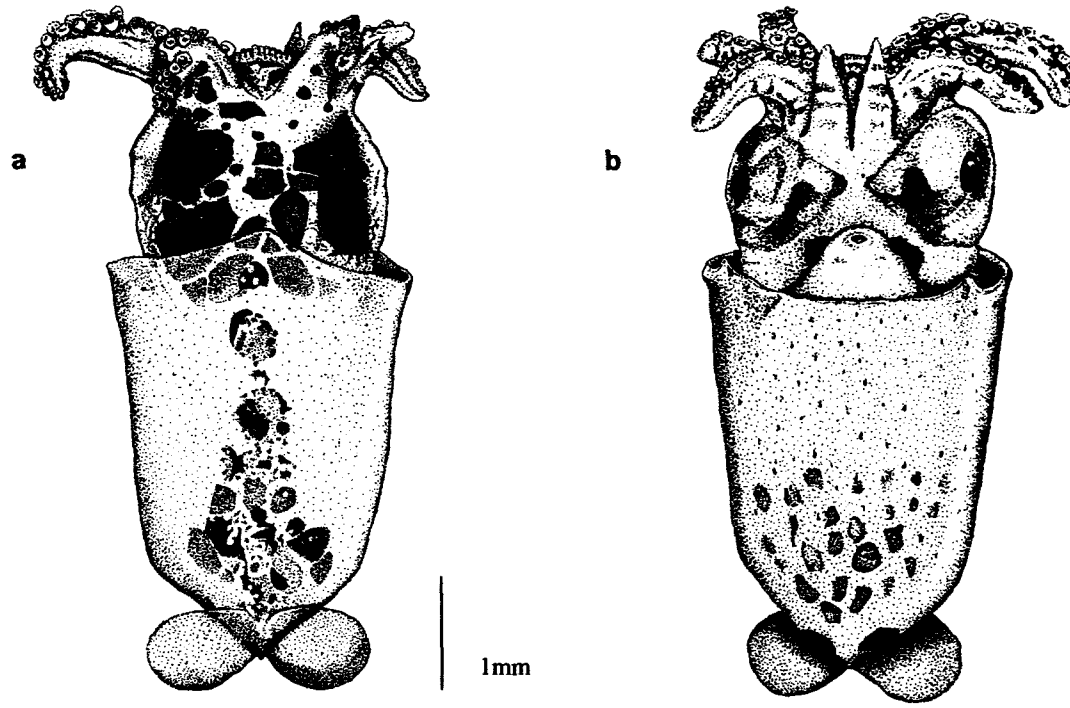


Fig. 11: ***Onykia carriboea***
Dorsal (a) and ventral (b) view of early juvenile (ML=3.7mm)

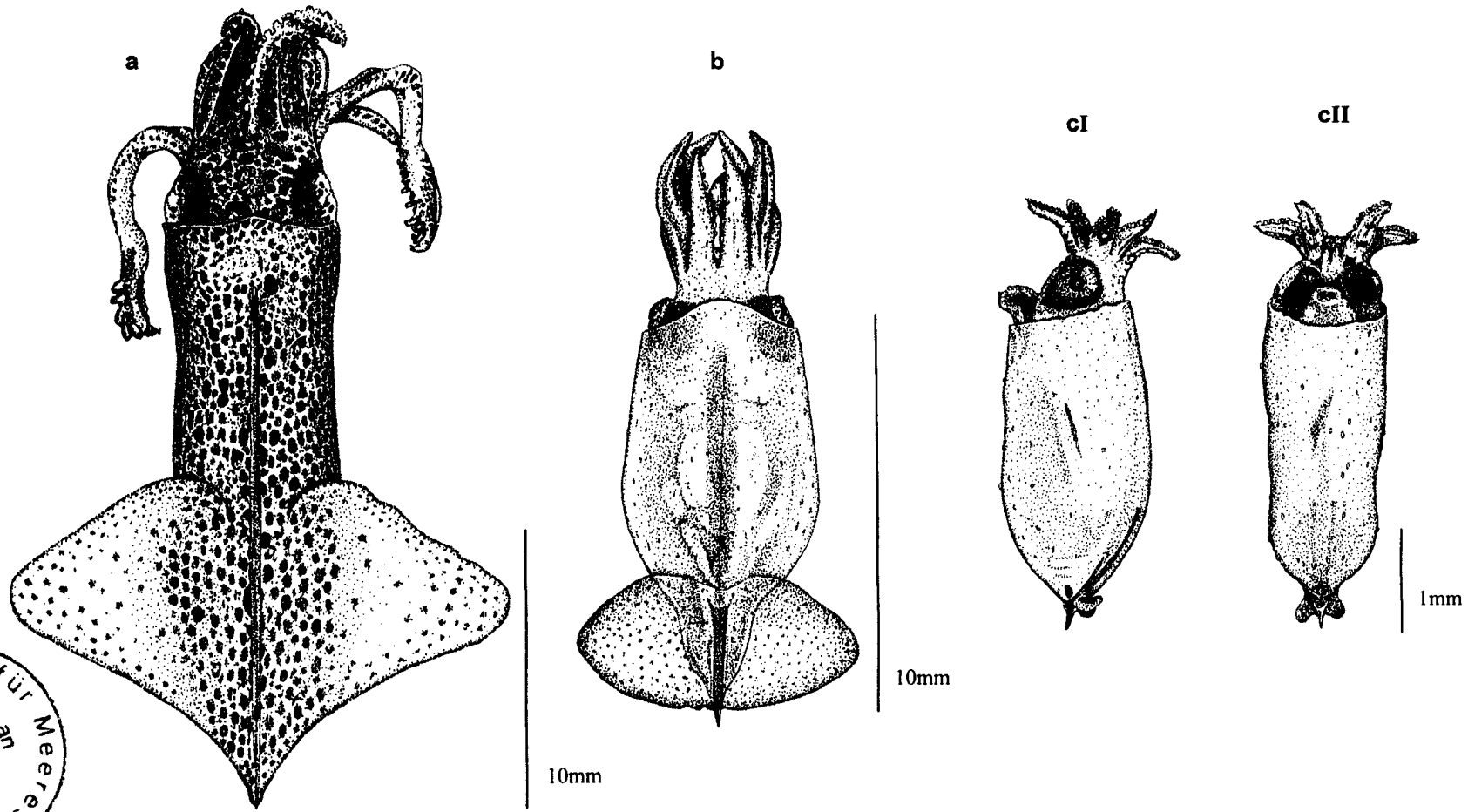


Fig. 12: ***Onychoteuthis banksii***
(a) Dorsal view (ML=23mm); (b) dorsal view (ML=11.7mm); (cI) lateral and (cII) ventral view of early juvenile (ML=2.7mm)

Family Chtenopterygidae

The Chtenopterygidae are a monotypic family with the single species *Chtenopteryx sicula* (Fig. 13). The species is distributed worldwide and easily identifiable at all developmental stages. In young specimens fins are small and start to develop muscular ribs (transversely elongated outline). Tentacles are short and the club spatulate; club suckers form a distinct circular pad. The fin length increases with size and almost extends along the whole mantle in adults. Fins are "ribbed": The muscular trabeculae are only joined by a membrane.

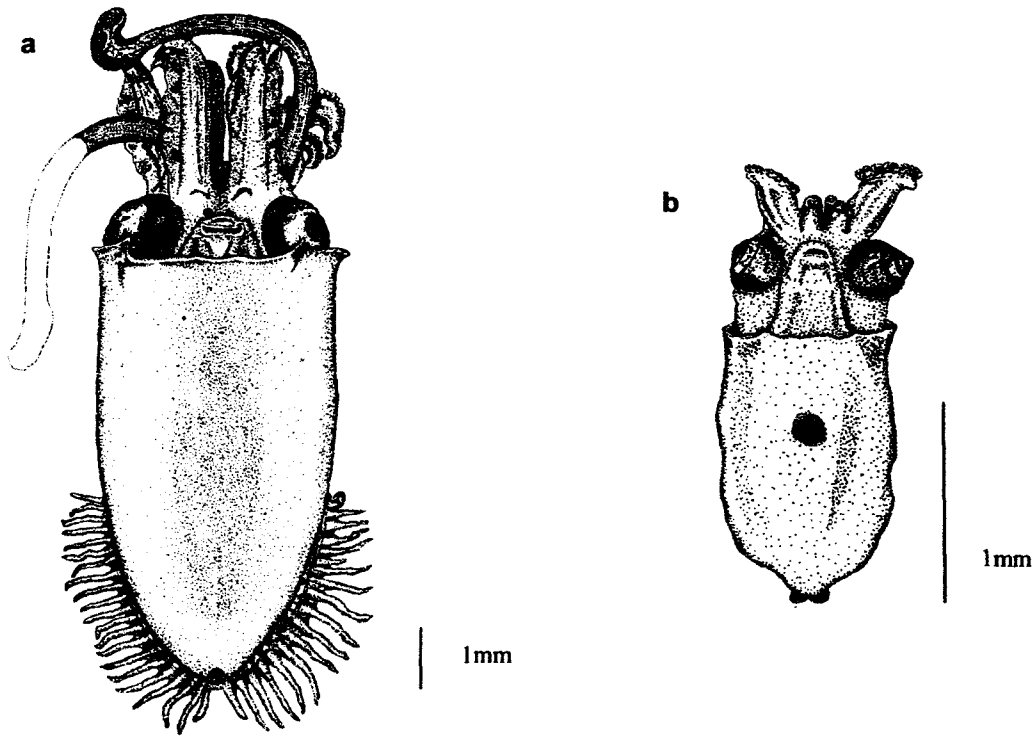


Fig. 13: ***Chtenopteryx sicula***
Ventral view of (a) juvenile (ML=7.5mm) and (b) hatchling (ML=1.3mm)

Family Thysanoteuthidae

The family Thysanoteuthidae is presently considered to be monotypic. The only species *Thysanoteuthis rhombus* (Fig. 14) is distributed worldwide from warm to temperate seas. Young specimens are recognisable by their (90° rotated) T-shape funnel locking-cartilage and their dense concentration of chromatophores on mantle, head and arms. Eyes are comparably small and broadly separated. Fins are small and rounded but extend more and more to the length of the mantle in growing specimens. Adults are large nektonic, muscular squids with rhomboidal fins. The characteristic funnel locking-cartilage remains unchanged in adults.

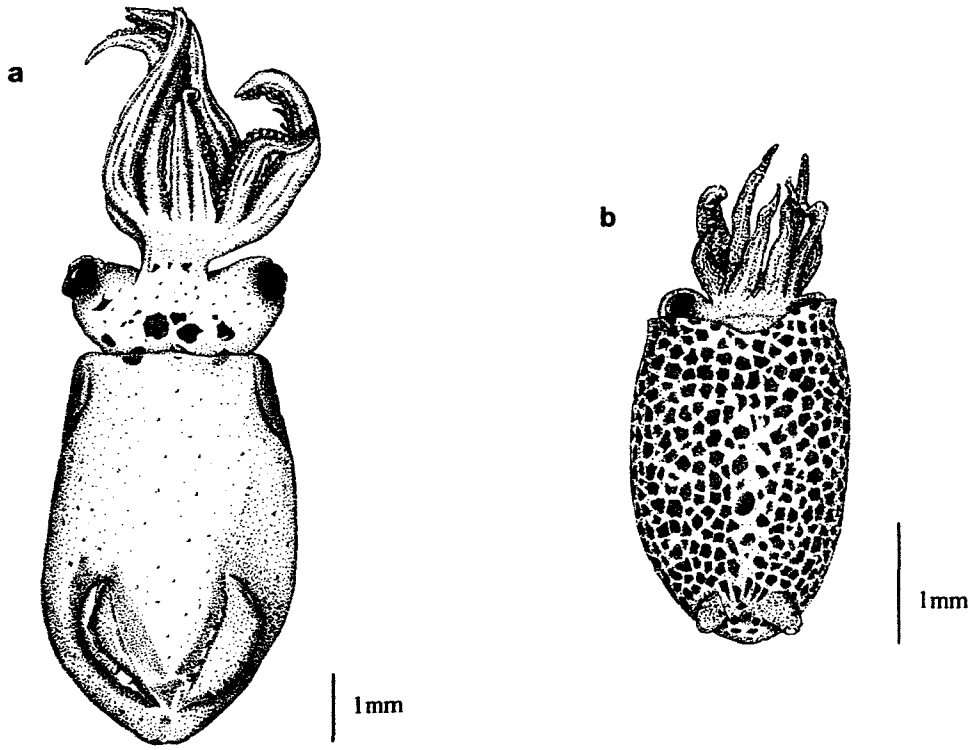


Fig. 14: ***Thysanoteuthis rhombus***
Dorsal view of juveniles (a) ML=5.6mm, (b) ML=2.7mm

Family Cycloteuthidae

Cycloteuthidae are distributed in the warm, subtropical to tropical waters of the oceans. Fins in adult specimens extend to more than 50% of mantle length. Early juveniles are characterised by a subtriangular funnel locking-cartilage and by eyes protruding on short stalks. Young Cycloteuthidae may be confused with young Octopoteuthidae because of similar fin size, tissue consistency and a few large suckers on the tentacular club. However, in Cycloteuthidae the fin musculature is separated by the gladius and suckers on the tentacular club exceed 12 in number.

Two genera are known within the family that can be distinguished by the characteristics given in Table 6.

Tab. 6: Key to the genera *Cycloteuthis* and *Discoteuthis*

	Cycloteuthis sp.	*Discoteuthis* sp.
fins	short (≤25% ML at 8.5mm ML), never more than 75% ML	long (50% ML at 5mm ML), grow up to 100% ML
tail	present in larger specimens	no tail
suckers on manus	suckers of equal size	suckers unequal in size
arm formula	2 = 3 ≥ 4 > 1	2 ≥ 3 > 4 > 1

Discoteuthis discus was the only species recognised in the subtropical eastern North Atlantic. It can be distinguished from the related species *D. laciniosa* by the absence of papillae on the ventral side of the mantle margins.

Family Octopoteuthidae

The Octopoteuthidae are cosmopolitan medium to large squids with a gelatinous body and a conical mantle. Similar to the Cycloteuthidae fins are very large and almost extend along the entire length of the mantle, but the fin musculature is not separated by the gladius. The funnel locking-cartilage is straight and moderately broad. The head is characterised by gelatinous tissue. In adult specimens tentacles are absent, whereas early juveniles have tentacles with a short, spatulate club with eight, partly very large suckers. Some arm tips, if not missing, bear photophores. Two genera are known within the family that can be distinguished by the characteristics given in Table 7.

Tab. 7: Key to the genera *Octopoteuthis* and *Taningia*

	Octopoteuthis sp.	*Taningia danae*
tentacular stalk	weak, gelatinous; tentacles lost at >12mm ML	robust; tentacles lost at >38mm ML
tentacular club	up to 8 large suckers	8 small suckers
arms	longer than tentacles, no hooks on arms before 2.5mm ML	short, robust; no hooks on arms before 5mm ML
photophores on ink sac	paired photophores by 15mm ML	large median photophore by 5mm ML

Although both genera are distributed worldwide the monotypic *Taningia danae* was the only species of this family that was identified in the samples of the subtropical eastern North Atlantic.

Family Bathyteuthidae

The Bathyteuthidae is a monogeneric family with currently three recognised species: *Bathyteuthis abyssicola, B. berryi, B. bacidifera.* Only one species (*B. abyssicola*) is distributed in the North Atlantic. It is a bathy- to mesopelagic squid and generally occurs between 700 to 2000m water depth. All known species are small-bodied (up to 7.5cm ML) and of a dark brown or maroon colour. Fins are small and paddle-shaped. At the base of each arm I-III a single photophore is imbedded into the tissue and all photophores are readily recognisable in early juveniles.

Family Brachioteuthidae

This family comprises small nektonic squids with a long neck and an elongated muscular mantle. Fins are paddle-shape and separated. Even young specimens show a distinctive swelling or hump on the dorsal surface of the head. Tentacles are large and relatively robust compared to the arms. There is no arm-crown stalk present. Brachioteuthidae are distributed circumglobally from the surface (young specimens) to the bathypelagial. The number of species in this family is not known and the family needs urgent revision.

Family Mastigoteuthidae

The Mastigoteuthidae are a monogeneric family. Two forms were recognised within the investigated area: *Mastigoteuthis* c.f. *atlantica* and *Idioteuthis* c.f. *hjorti* (formerly *Mastigopsis hjorti*).

Young specimens of this genus are identifiable by their elongated mantle, the long gladius, that is projecting posterior to the fins as a long pointed tail, the anteriorly protruding eyes and the thick (thicker than the arms) tentacular stalks. Tentacular clubs bear more than 4 rows of suckers. In juvenile to adult specimens the funnel locking-cartilage is recognisable as an oval structure with inward projecting knobs. Nevertheless, the posterior and the medial tragus are mostly poorly developed.

Family Chiroteuthidae
(incl. Grimalditeuthidae)

The family Chiroteuthidae is currently known to include four genera: *Chiroteuthis*, *Asperoteuthis*, *Grimalditeuthis* and *Planctoteuthis* (Young, 1991). Its most distinctive feature is the "doratopsis" paralarvae, which is defined by e.g. the following characteristics:

- elongated chambered neck
- a gladius that extends posteriorly beyond the fins
- vesiculate arms in advanced stage
- greatly elongated ventral arms in advanced stage

The genus ***Planctoteuthis*** is a synonym to ***Valbyteuthis***, which is now recognised as the early life stage of *Planctoteuthis*. *Chiroteuthis* (Fig. 15) and *Valbyteuthis* (*Planctoteuthis*) can be distinguished by the characteristics listed in Table 8.

The genus ***Grimalditeuthis*** was formerly put into the separate family Grimalditeuthidae and is treated like this in the identification key. Early life stages from this genus are not known so far, so that the doratopsis characteristics do not meet for subadult *Grimalditeuthis*. At this stage the tail is maintained and the gladius still extends well posterior to the fins. The funnel-mantle locking-cartilages fuse, similar to the Cranchiidae. Another distinguishing feature is the vesiculate region surrounding the posterior end of the mantle. The only species described so far is *Grimalditeuthis bonplandi*.

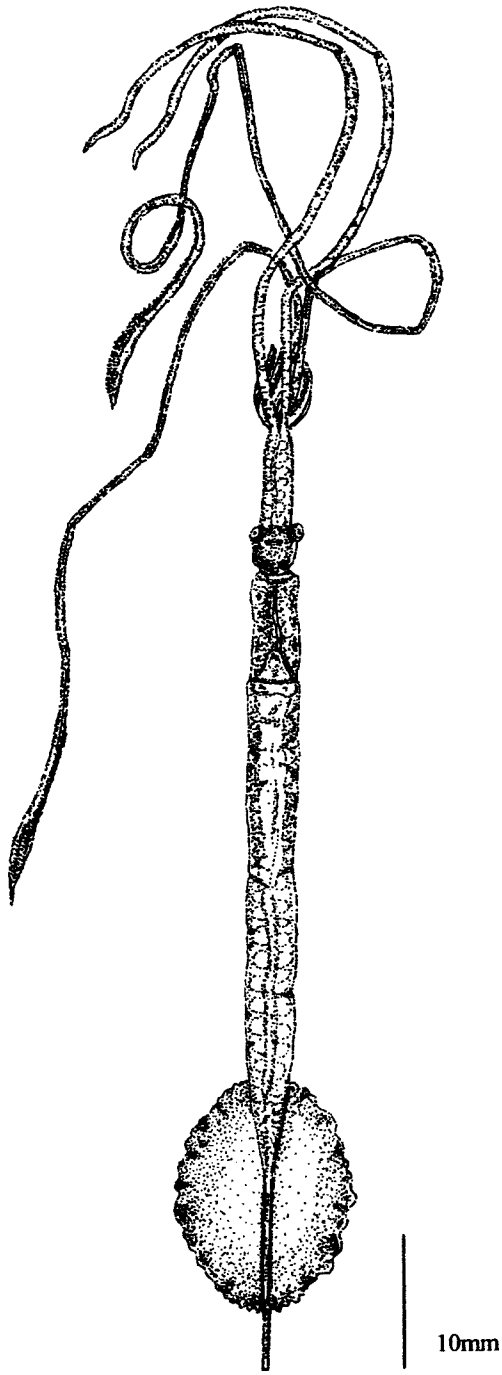


Fig. 15: ***Chiroteuthis* sp.**
Ventral view, larval features still retained (ML=56mm)

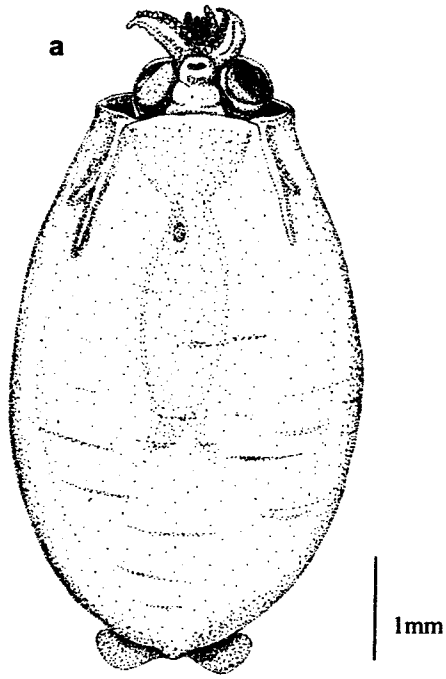
Tab. 8: Key to genera *Chiroteuthis* and *Valbyteuthis*

	Chiroteuthis sp.	*Valbyteuthis* sp.
Mantle	Long, slender, spindle shape	Relatively broad, bead-like shape
Arm-crown stalk	Short relative to neck length	As long or longer than neck
Tentacular stalkes	Suckers on oral surface (rarely naked)	naked

Family Cranchiidae

Cranchiids are distributed worldwide, from the Subarctic to the Antarctic. All species of this family exhibit an ontogenetic descent, as maturation occurs in deep waters down to 2000m water depth. Specimens are characterised by a thin walled mantle, often semigelatinous, and the permanently fusion of the mantle with the funnel locking-cartilage as well as with the head in the nuchal region. The family is currently under revision by N.Voss. Two subfamilies, 13 genera and more than 60 species are recognised so far.

Most of the cranchiid species display a special paralarval stage, that is characterised by stalked eyes and a short to long arm-crow stalk. Identification of early juveniles may be problematic and for details the relevant literature has to be consulted (Voss, 1980; Voss et al., 1992). An overview about an assortment of genera and species, occurring in the subtropical North Atlantic, and their respective characteristics is given in Table 9.



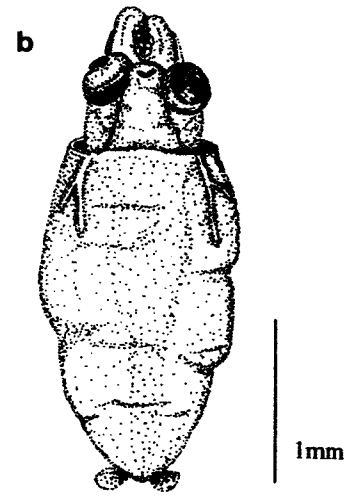


Fig. 16: Subfamily Cranchiinae
Ventral view of
(a) ***Cranchia scabra*** (ML=5.5mm),
(b) ***Liocranchia* sp.** (ML=2.2mm)

Fig. 17: Subfamily Taoninae
Bathothauma lyromma
Early juvenile (ML=6.9mm)

Tab. 9: Key to the genera of the family Cranchiidae found in the subtropical eastern North Atlantic

	mantle	gladius/ lanceola	fins	cartilaginous strips (on ventral surface of mantle)	arm crown stalk	eyes	other features
Sub-fam. Cranchiinae:							
Cranchia scabra (Fig. 16a)	stocky, often near-round	–	small, separated, paddle-shaped fins; unite dorsally with growth	inverted V-shape, non-tubercular (apparent not before 10-15mm ML)	no stalk	sessile, but protruding	scattered cross-shaped tubercles on mantle, few in early juveniles
Liocranchia (Fig. 16b)	stocky, spindle shaped	–	small, separated, paddle-shaped fins; fuse dorsally with growth	inverted V-shape, tubercular (extends from each funnel-mantle fusion)	no stalk	sessile, but protruding	arms very short
Leachia	moderately stout, spindle-shaped, but elongates with growth	gladial spine, projects between fins	transversely elliptical	single tubercular strip (extends from each funnel-mantel fusion)	long stalk	stalked	details of tubercu-lar strips important for species identification
Sub-fam. Taoninae:							
Helicocranchia (Fig. 18-20)	elongated, cylindrical, often with mucous outer layer	gladius projects dorsally free of mantle	small, paddle-shaped, insert on posterior tip of gladius	–	short stalk	oval, with pronounced ventral rostrum on short stalkes	very large funnel
Bathothauma (Fig. 17)	elongated, sac-shaped, rounded posteriorly	gladius expanded at right angle to mantle	small, paddle-shaped, widely set apart (on gladius)	–	long stalk	oval, on long stalkes, with ventral rostrum	tentacles short and robust in early juveniles
Liguriella	firm, spindle shaped	blunt-pointed, moderately broad, diamond-shaped lanceola	paddle-shaped, become oval with growth	–	medium to long stalk	oval, on long stalkes, with distinct short ventral rostrum	tentacles short and firm in early juveniles but elongate with growth
Taonius	elongated, narrow, cone-shaped	very elongated, narrow, diamond-shaped lanceola	short, lanceolate, but are extending along the lanceola with growth	–	moderately long stalk	oval, on very long stalks	specimens appear "stretched"
Megalocranchia	stocky, spindle-shaped, often with mucous outer layer	moderately narrow, diamond-shaped lanceola	small, become rounded with growth and extend to the mantle margins	–	long stalk	oval, on long stalkes, with short ventral rostrum	compound photo-phore on ventral surface of digestive gland (~25mm ML)

One of the most abundant cranchiids in the oceanic parts of the North Atlantic is the genus ***Helicocranchia***. It is probably composed of about 14 species (N.Voss, pers. comm.). In the subtropical eastern North Atlantic two species were identified, that can be distinguished by the following characteristics:

Tab. 10: Key to the species *Helicocranchia pfefferi* and *Helicocrancia papillata*

	Helicocranchia pfefferi	*Helicocranchia papillata*
posterior end of gladius	long, narrow rostrum (Fig. 18, Ia, b)	short, broad based rostrum (Fig. 18, IIa, b)
fins (interspecies comparison)	larger	smaller
funnel organ	Ventral pads: L-shaped (Fig. 18, Ic)	Ventral pads: Curved club-shaped (Fig. 18, IIc)
arms	III: no suckers disproportionally enlarged	III: enlarged suckers on median portions (>7mm ML)
tentacles	moderately long and robust	long and delicate: >100% ML (>10mm ML)
tentacular club: Dactylus	Suckers gradually enlarged from dorsal to ventral margins	Suckers gradually enlarged from dorsal to ventral margins
tentacular club: Manus	Median two rows of suckers slightly enlarged	Five or more suckers of ventral row disproportionally enlarged

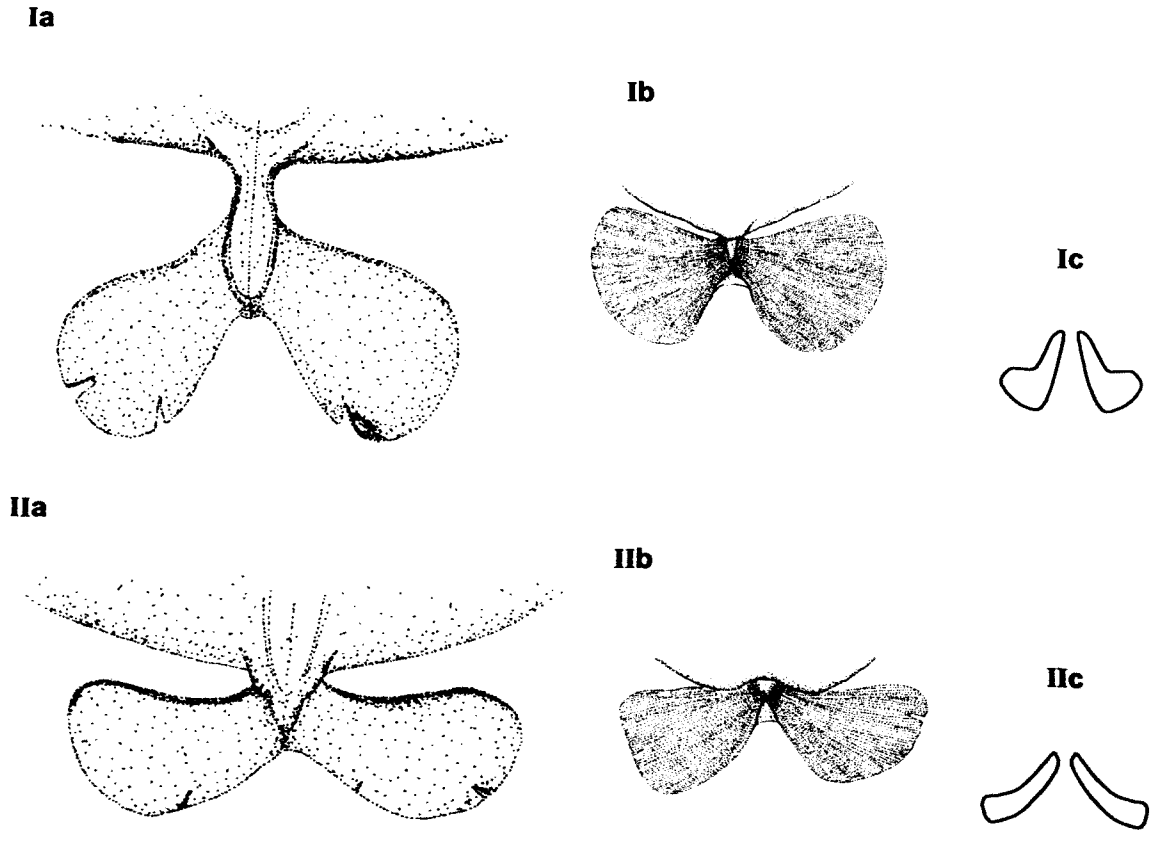


Fig. 18: Posterior end of (I) ***Helicocranchia pfefferi*** (ML=8.5mm) and (II) ***Helicocranchia papillata*** (ML=9mm). (a) Dorsal view, showing the projecting rostrum of the gladius; (b) ventral view of the same. (c) Ventral pads of the funnel organ

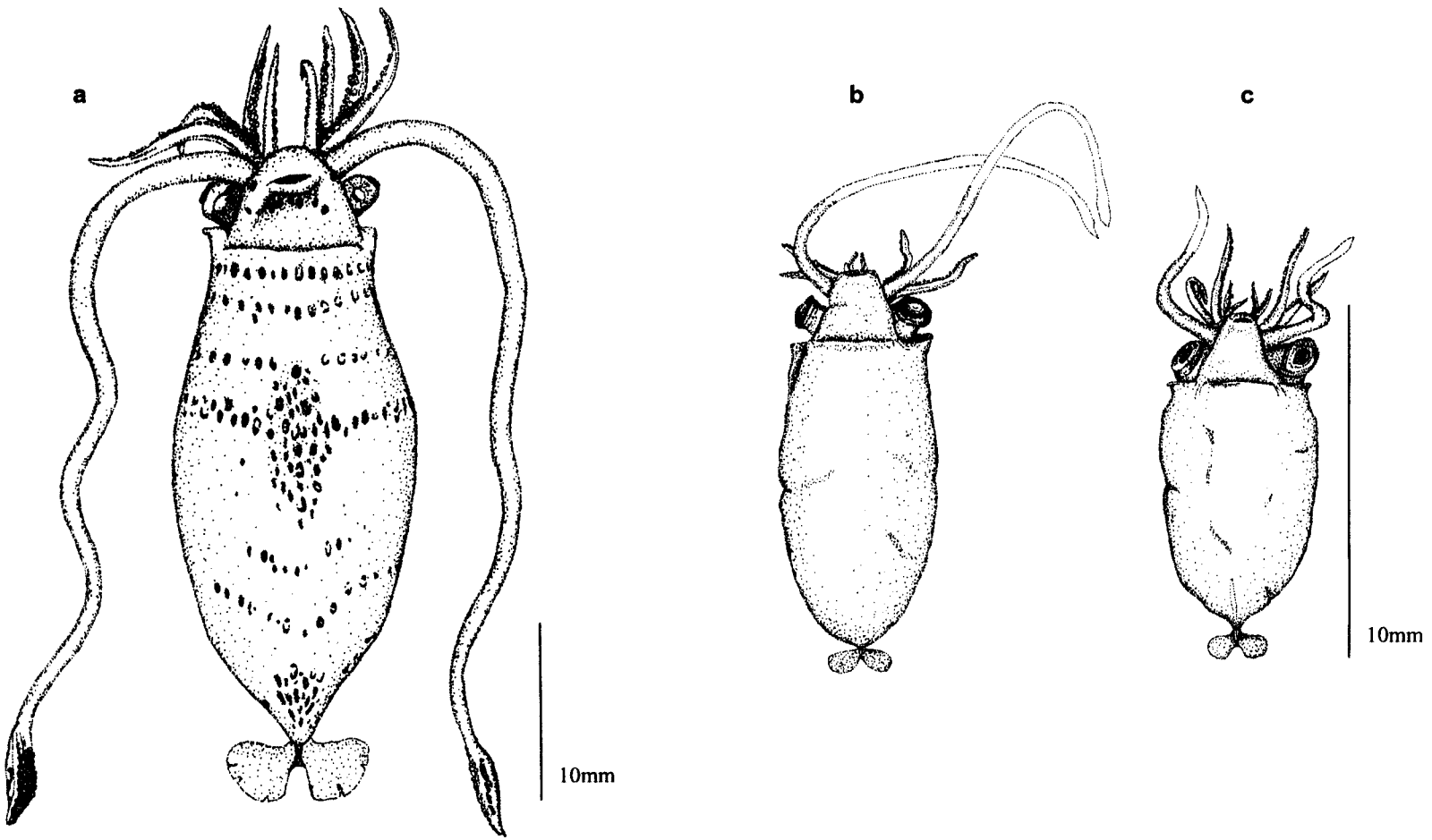


Fig. 19: ***Helicocranchia pfefferi***
Ventral view: (a) ML=30mm, (b) ML=8.5mm, (c) ML=6.9mm

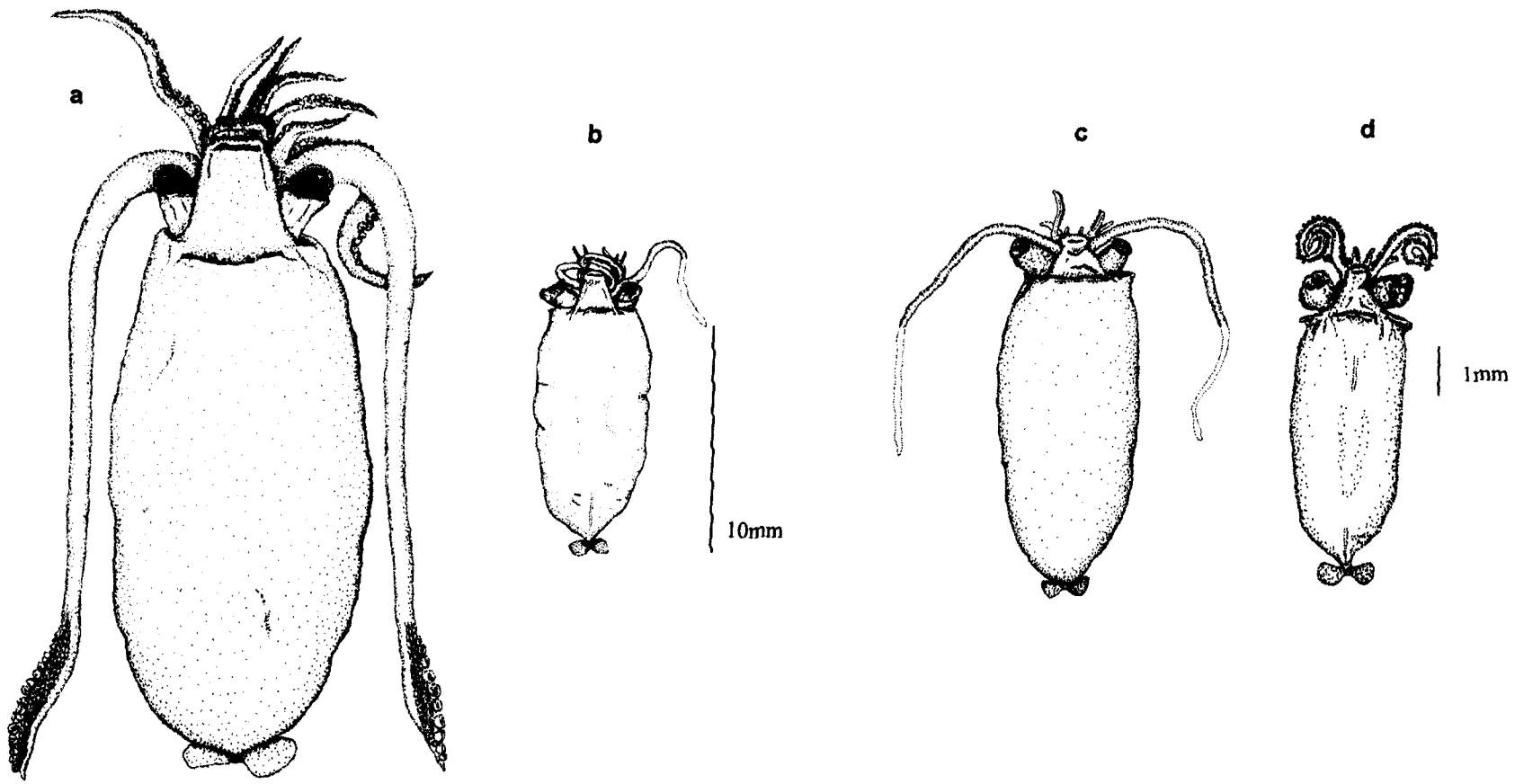


Fig. 20: ***Helicocranchia papillata***
Ventral view: (a) ML=24mm, (b) ML=10.7mm, (c) ML=9mm, (d) ML=6.2mm

Order Octopoda: Suborder Incirrina

All families within this octopod suborder have in common, that fins and arm cirri are absent. The skin of all specimens carries functional, chromatophores. The families identified in the subtropical eastern North Atlantic can be distinguished by the characteristics described below.

Tab. 11: Key to the families of the suborder Incirrinae, found near seamounts in the subtropical eastern North Atlantic

	mantle	arms	arm suckers	funnel locking-cartilage	eyes	male specimens	other features
Alloposidae (monotypic: *Alloposus mollis* / *Haliphron atlanticus*)	gelatinous, short, uniformly and densely pigmented	relatively short, connected by deep web	uniserial proximally, biserial distally (to edge of web)	hook like, only slightly developed	hemispherical, large, diameter about 40% ML	right arm III hectocotylized, develops in pouch	
Argonautidae (monogeneric: *Argonauta argo*), Fig. 25	muscular, firm	web weakly developed; hatchlings with brachial membrane	uniserial in hatchlings; biserial and small in growing specimens	specialised, knob-like	small, slightly anterolaterally directed	dwarfed; hectocotylized arm III in pouch; even visible in paralarvae	females with thin, calcareous shell; 1st arm longer, secreting the shell
Bolitaenidae (*Eldonella pygmaea*), Fig. 21	gelatinous, pigmented; jelly-like outer coating in young specimens	shorter than mantle; arms III slightly elongated	uniserial, generally small	absent	medium sized, elliptical, laterally directed	right or left arm III hectocotylized: enlarged suckers	elongated ovoid digestive gland
Octopodidae (*Octopus sp.*), Fig. 26	muscular, firm; hatchlings with Koelliker´s bristles	short, elongate slightly during growth; no web	uniserial in hatchlings; biserial in growing specimens	simple	small, anterolaterally directed	left or right arm III hectocotylized: mature males benthic	benthic settling at about 6-10mm ML
Ocythoidae (monotypic: *Ocythoe tuberculata*), Fig. 24	muscular; ventral side of females with tubercles and ridges (reticulate)	I and IV greatly elongated; no web; no brachial membrane in hatchlings	small suckers; biserial	specialised	medium sized, elliptical	dwarfed; hectocotylized arm III in stalked pouch	funnel very long; ventral pair of cephalic water pores
Tremoctopodidae (*Tremoctopus violaceus*), Fig. 22	muscular, thick, dorsally densely covered with chromatophores	I and II greatly elongated; web dorsally very deep, ventrally ± absent	small, numerous suckers; biserial; young: very large in dorsal arms	specialised	large, surrounded by gold iridophores	dwarfed; hectocotylized arm III develops in pouch below eye	cephalic water pores; in paralarvae: brachial membrane present
Vitreledonellidae (monotypic: *Vitreledonella richardi*), Fig. 23	semigelatinous, sac-like; jelly-like coating in young specimens	body to arm ratio 2:1; all arms connected by deep web	uniserial, widely spaced	absent	small, rectangular, laterally directed	tip of left arm III hectocotylized	long, slender digestiv gland, situated posterior to stomach

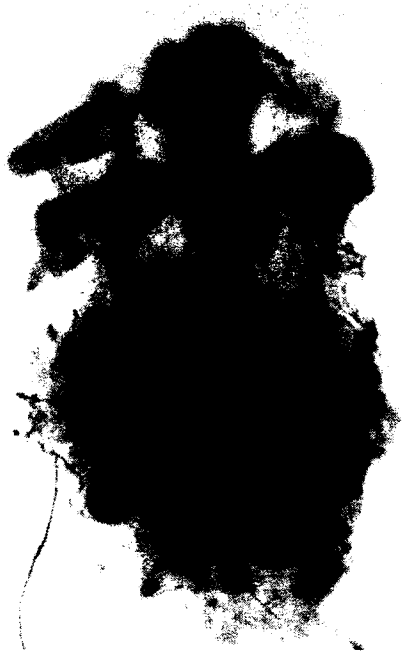


Fig. 21: ***Eledonella pygmaea***
Hatchling (ML=1.7mm);
cosmopolitan species, in tropical to
temperate waters; meso- to bathypelagic

Fig. 22: ***Tremoctopus violaceus***
Female juvenile (ML=2.2mm);
cosmopolitan species, in tropical to temperate waters;
epi- to upper mesopelagic

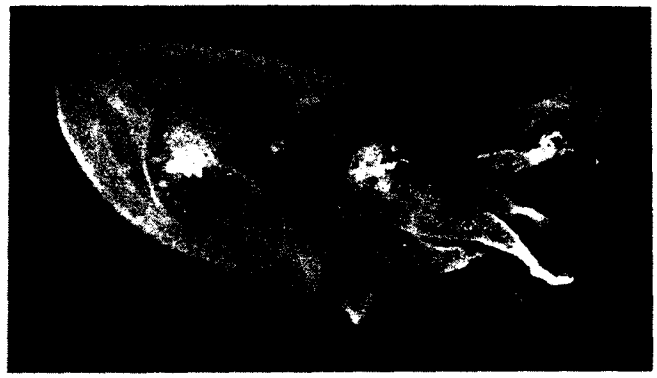
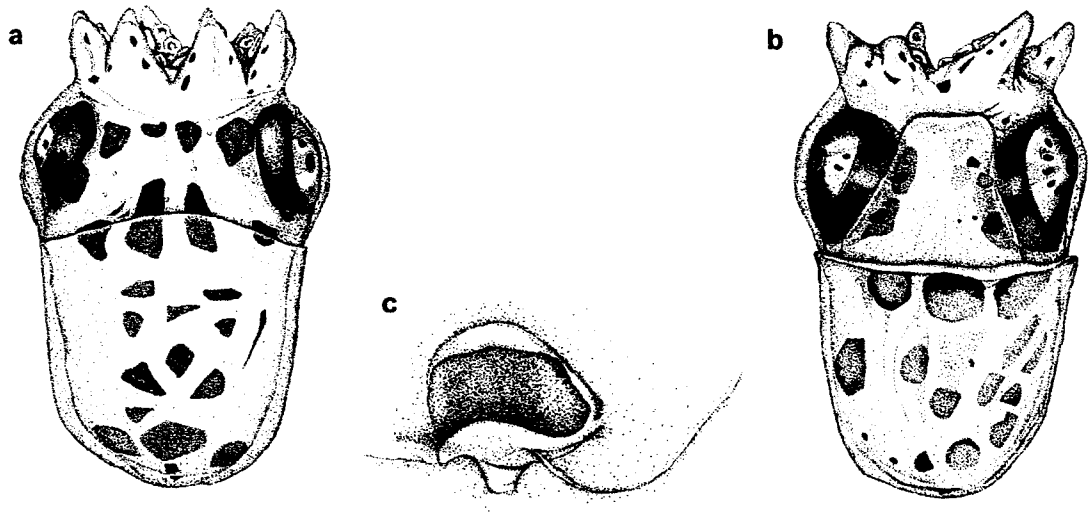


Fig. 23: ***Vitreledonella richardi***
Female juvenile (ML~30mm);
cosmopolitan species, in tropical to
temperate waters; meso-to bathy-
pelagic

Fig. 24: ***Ocythoe tuberculata***
Female juvenile (ML~18mm);
cosmopolitan species, in tropical to
temperate waters; epipelagic



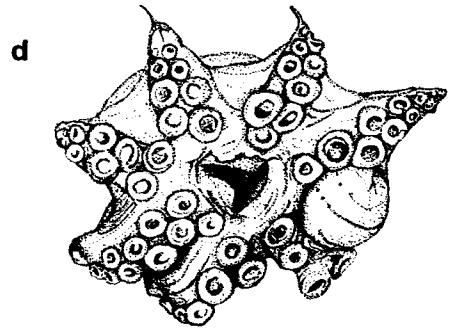


Fig. 25: ***Argonauta argo***
Dorsal (a) and ventral (b) view of paralarva (ML=1.4mm), (c) funnel locking cartilage of the same specimen
(d) Arm crown of juvenile male with hectocotylus enclosed in sac (ML=2mm)

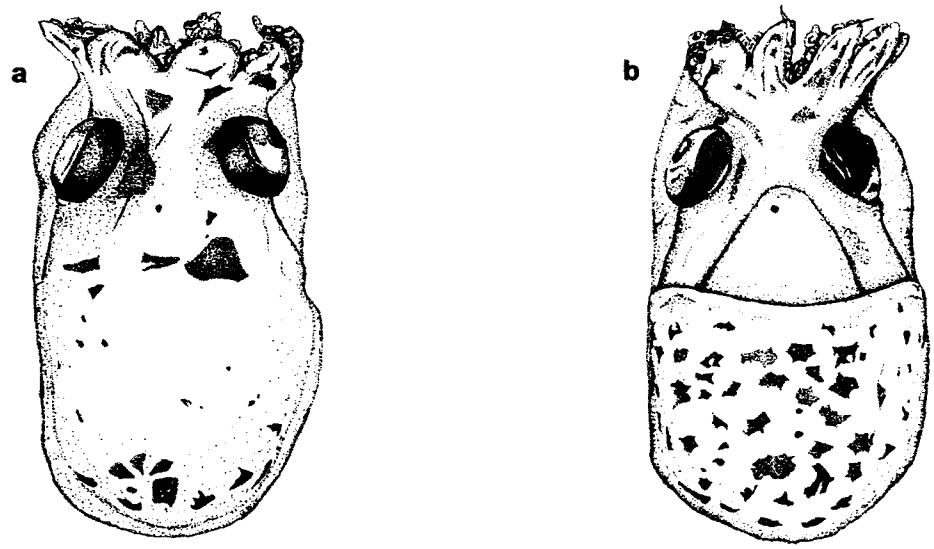


Fig. 26: ***Octopus* sp.**
Dorsal (a) and ventral view (b) of paralarva (ML=1.5mm)

8. Glossary

Arm crown = encompasses all circumoral appendages, i.e. arms and tentacles. In many juvenile squids and certain species (e.g. *Brachioteuthis*, *Chiroteuthis*) the arm crown is "stalked", i.e. the arm crown is situated on an elongation of the head.

Arm formula = ratio between the length of the four arm pairs

Buccal mass = thickened tissue that encircles the mouth

Chromatophores = organs, located beneath or within the integument, and forming the colour patterns of cephalopods. Chromatophores are muscle- and nerve-innerved and, thus, provide the colour- and colour-pattern changes.

Cornea = thin, transparent membrane that covers the eyes of myopsid squids and Sepioidae. A cornea is missing in oegopsid squids, the eye has contact to the seawater.

Funnel locking-cartilage = a cartilaginous structure on each ventrolateral side of the funnel base. It locks the funnel and mantle together (see: mantle locking-cartilage) in order to close the anterior part of the mantle for locomotion (jet-propulsion). The funnel locking-cartilage may serve for species identification, as it is characterised by a species specific shape with grooves and pits.

Gladius = stabilising chitinous structure on the dorsal midline of the mantle in teuthoids and sepioids (not Sepiidae). It is homologous to the outer shell of ancestral forms (see also "Lanceola").

Hectocotylus = modification of one (or more) arms of male cephalopods for transferring spermatophores to the females. A hectocotylus may be characterised by the arm shape, specialised suckers etc.. Not all cephalopod species show these modifications in males.

Lanceola = the posterior expanded portion of the gladius (see above), e.g. in the family Cranchiidae

Light organ = see: Photophores

Mantle locking-cartilage = the matching piece to the funnel locking-cartilage (see above). The cartilaginous structure can be found on the ventrolateral internal side of the mantle.

Nuchal region = dorsolateral area of the posterior part of the head, usually covered by the mantle. In the family Cranchiidae the mantle and head are fused in this area.

Paralarva = an introduced term by Young & Harman (1988) for early life stages of cephalopods that meet certain morphological and ecological criteria. Most cephalopods lack real "larval" modifications in their early life development. Early stages of cephalopods that differ in habit, habitat and/or often morphology from their adults are, thus, proposed to be defined as "paralarvae" to fill the gap in terminology. Most but not all pelagic cephalopods and octopods do fall in this category. For further information, refer to Young & Harman (1988).

Photophores = an organ that produces bioluminescence by means of a biochemical reaction (self-generated) or through luminescent bacteria. Photophores can be located within the integument but is also found on e.g. the intestinal tract (e.g. *Hyaloteuthis pelagica*, *Megalocranchia* sp.).

Proboscis = a trunk-like structure in the early life stages of Ommastrephidae ("Rhynchoteuthion", see below). In the paralarvae development the proboscis divides into the two tentacles of the adults.

Rhynchoteuthion = a distinctive larval form of the family Ommastrephidae. It is characterised by the proboscis (see above), which is already present in hatchlings.

Rostrum = an extension of the gladius or cuttlebone which may project sharply out of the posterior part of the mantle.

Tragus = a small projection from the inner wall of the funnel locking-cartilage in certain families (e.g. Chiroteuthidae and Mastigoteuthidae).

Web = A fold of the skin that extends between the arms in some octopods (e.g. Vitreledonellidae) and a few squids (e.g. Histioteuthidae). This muscular skin fold connects all or only certain arm pairs and may extend to the arm tips as a deep web (e.g. Alloposidae).

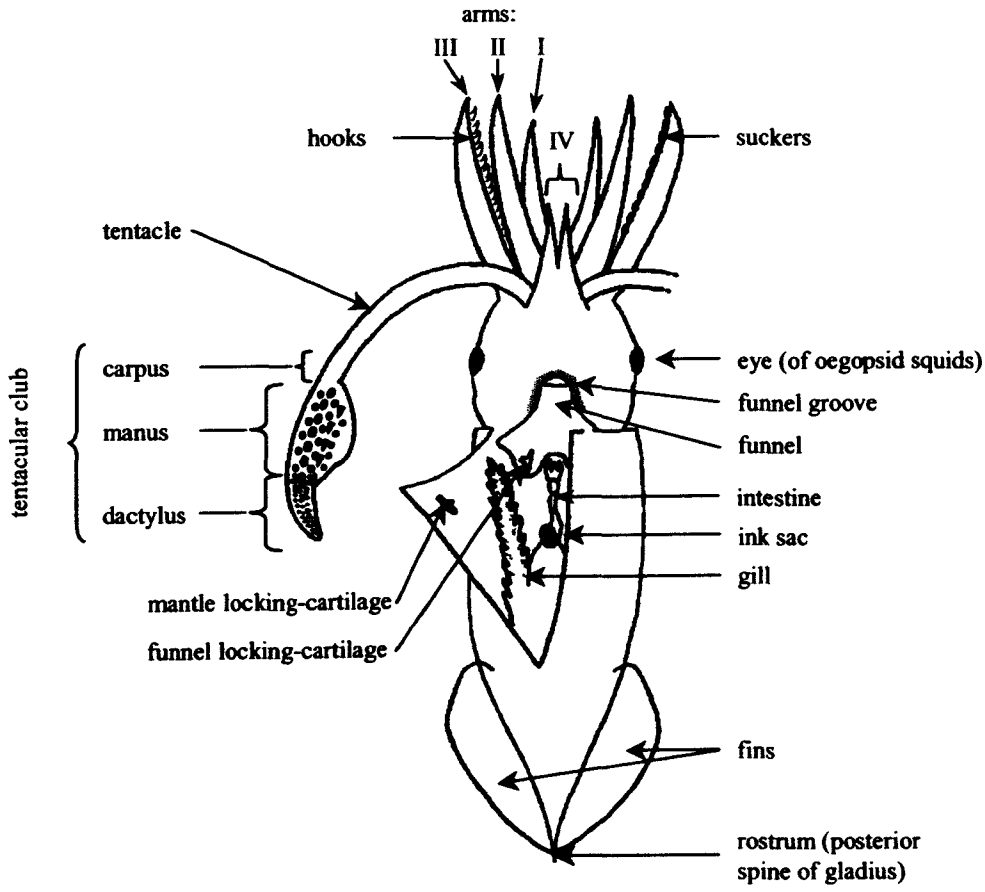


Fig. 27: Ventral view of schematic teuthoid squid

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